RESEARCH ARTICLE

Predictive habitat suitability models for nesting woodpeckers following wildfire in the Sierra Nevada and Southern Cascades of California

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ABSTRACT

Woodpeckers are often focal species for informing management of recently burned forests. Snags generated by wildfire provide key nesting and foraging resources for woodpeckers, and nest cavities excavated by woodpeckers are subsequently used by many other species. Habitat suitability models applicable in newly burned forest are important management tools for identifying areas likely to be used by nesting woodpeckers. Here we present and test predictive models for mapping woodpecker nest-site habitat across wildfire locations that can be used to inform post-fire planning and salvage logging decisions. From 2009 to 2016, we monitored 313 nest sites of 4 species—Black-backed Woodpecker (*Picoides arcticus*), Hairy Woodpecker (*Dryobates villosus*), White-headed Woodpecker (*D. albolarvatus*), and Northern Flicker (*Colaptes auratus*)—from 3 wildfires in the Northern Sierra Nevada and Southern Cascades 1–5 yr after fire. Using these data, we developed habitat suitability index models that compared nest vs. non-nest sites for each species using (1) exclusively remotely sensed covariates, and (2) combinations of remotely sensed and field-collected covariates. We emphasized predictive performance across wildfire locations when selecting models to retain generalizable habitat relationships useful for informing management in newly burned locations. We identified models for all 4 species with strong predictive performance across wildfire locations despite notable variation in conditions among locations, suggesting broad applicability to guide post-fire management in the Sierra Nevada region. Top models for nest-site selection underscored the importance of high burn severity at the local scale, lower burn severity at the 1-km scale, mid-sized nest-tree diameters, and nest trees with broken tops. Models restricted to remotely sensed covariates exhibited similar predictive performance as combination models and are valuable for mapping habitat across entire wildfire locations to help delineate project areas or habitat reserves. Combination models are especially relevant for design of silvicultural prescriptions.

Keywords: conservation, forest management, predictive performance, salvage logging, species distribution, wildfire

Modelos predictivos de aptitud del hábitat para carpinteros que anidan luego de incendios forestales en la Sierra Nevada y las Cascadas del Sur de California

RESUMEN

Los carpinteros son usualmente usados como especies focales para informar el manejo de bosques recientemente quemados. Los tocones generados por los incendios brindan recursos claves de anidación y forrajeo para los carpinteros, y los nidos excavados por los carpinteros son luego usados por muchas otras especies. Los modelos de aptitud del hábitat aplicables a bosques recientemente quemados son herramientas de manejo importantes para identificar el uso probable por parte de los carpinteros que anidan. Aquí presentamos y evaluamos modelos predictivos para mapear los hábitats aptos para ser usados como sitios de anidación por los carpinteros a través de las ubicaciones incendiadas que pueden usarse para planificar las tareas posteriores al incendio y las decisiones de aprovechamiento forestal de salvataje. Desde 2009 a 2016, monitoreamos 313 sitios de anidación de cuatro especies—*Picoides arcticus*, *Dryobates villosus*, *D. albolarvatus* y *Colaptes auratus*—en tres incendios forestales en el norte de la Sierra Nevada y las Cascadas del Sur, 1–5 años posteriores al fuego. Usando estos datos, desarrollamos modelos de indexación de aptitud del hábitat que comparan sitios con y sin nidos para cada especie usando (1) co-variables censadas exclusivamente de forma remota y (2) combinaciones de co-variables censadas de forma remota y colectadas a campo. Enfatizamos el desempeño predictivo a través de las ubicaciones de los incendios forestales al seleccionar modelos para mantener relaciones de hábitat generalizables, útiles para informar a los gestores en las ubicaciones recientemente quemadas. Identificamos modelos para las cuatro especies con un desempeño predictivo fuerte a través de las ubicaciones de los incendios forestales, a pesar de la notable variación en las condiciones entre las ubicaciones, sugiriendo la amplia aplicabilidad para guiar el manejo post incendio en la región de la Sierra Nevada. Los mejores modelos para la selección de los sitios de anidación subrayaron la importancia de la alta gravedad de las quemas a la escala local, de la menor gravedad de las quemas a la escala de 1 km, de árboles de anidación de diámetro de tamaño intermedio y de árboles de anidación con las puntas

quebradas. Los modelos restringidos a las co-variables censadas de forma remota mostraron un desempeño predictivo similar que los modelos combinados, y son valiosos para mapear el hábitat a través de ubicaciones totalmente afectadas por incendios forestales y para ayudar a delinear áreas de proyectos o reservas de hábitat. Los modelos combinados son especialmente relevantes para diseñar las prescripciones silviculturales.

Palabras clave: aprovechamiento forestal de salvataje, conservación, desempeño predictivo, distribución de especies, incendio forestal, manejo forestal

INTRODUCTION

In the western United States, an ongoing debate concerns how to manage fire and burned forested landscapes (Long et al. 2014, Hessburg et al. 2016, DellaSala et al. 2017). A central theme of the debate centers on removal of fire-killed and injured trees—salvage logging—for primarily economic benefits and to reduce the risk of future fires. Additionally, timber may be felled and harvested after fire to reduce hazards to workers, recreational users, and infrastructure (Peterson et al. 2009). Salvage logging, however, can negatively impact disturbance-associated wildlife populations, especially those that use snags (standing dead trees) for nesting, foraging, or other activities (e.g., woodpeckers; Hutto and Gallo 2006, Saab et al. 2007, Rost et al. 2013). Decisions about salvage logging are made on accelerated timescales, as the timber rapidly deteriorates and loses value (Prestemon et al. 2006, Lowell et al. 2010), requiring managers to quickly identify areas with wildlife habitat that provide key resources for species of management interest.

Habitat suitability models can inform management decisions by describing key habitat requirements and predicting species distributions (e.g., Maiorano et al. 2006, Bellamy et al. 2013). Habitat suitability models quantify statistical relationships between environmental features and known species occurrences, which provides the basis for prediction. Often, available data discriminate environmental conditions at occurrence from reference sites (e.g., use–availability data), so predictions are best interpreted as relative indices (Hirzel et al. 2006, Russell et al. 2007, Latif et al. 2016). Habitat suitability indices (HSIs) typically range from 0 to 1, indicate relative likelihood of species occurrence, and are often translated into suitability categories (e.g., low, moderate, and high) to facilitate application (Hirzel et al. 2006, Liu et al. 2013). Forest managers informed by HSI models could limit impactful activities (e.g., salvage logging) in areas of higher suitability to meet conservation targets.

The utility of habitat models for informing post-fire planning depends in part on how efficiently models can be applied to recently burned areas. Managers frequently require maps to identify areas suitable for wildlife; these maps can be used to delineate project areas or habitat reserves. Maps are most easily generated by models developed with remotely sensed data available for entire burned areas (Franklin 2009, Elith et al. 2010). However, limitations in the resolution of remotely sensed data may preclude modeling of finer-scale habitat relationships and limit model performance (Kerr and Ostrovsky 2003, Russell et al. 2007). Finer-scale field-collected habitat data, such as snag sizes, densities, species, and condition, may be important for modeling wildlife–habitat relationships (Russell et al. 2007). The expense and time of data collection, however, limits the efficiency of models developed with field-collected data for mapping habitat over broad spatial extents, such as wildfire locations.

Given limited time and funding for new population surveys, managers may want to quickly apply habitat suitability models as wildfire occurs outside where models were originally developed (Latif et al. 2013, 2016). Biotic interactions, local adaptation, and behavioral rules governing habitat selection, however, can give rise to spatial variability in environmental relationships, which can limit model applicability (Araújo and Luoto 2007, Morrison 2012, Aarts et al. 2013). Hence, models typically exhibit poorer predictive performance when applied beyond where originally developed, so practitioners increasingly recommend evaluating model transferability explicitly across space to limit overconfidence in application (Wiens et al. 2008, Heikkinen et al. 2012, Wenger and Olden 2012). For models to be most useful to managers, model development with data from multiple locations will allow broader applicability and evaluation of transferability to new wildfires (Saracco et al. 2011, Latif et al. 2013, 2016; Tingley et al. 2016). Additionally, explicitly favoring predictive performance when selecting models (sensu Wiens et al. 2008) could benefit model applicability in new wildfire locations.

Woodpeckers often represent focal species for informing management of recently burned forests, largely because snags generated by wildfire provide crucial nesting and foraging resources for woodpeckers, and cavities excavated by nesting woodpeckers are subsequently used by many other species (i.e. nest webs; Martin et al. 2004, Virkkala 2006, Tarbill et al. 2015, DellaSala et al. 2017). Therefore, managing for multiple woodpecker species can favor conservation of a range of habitat conditions that benefit cavity-associated and deadwood-associated biodiversity. Numerous researchers have developed habitat suitability models for woodpeckers in mixed conifer forests of the western United States to inform post-fire management (Russell et al. 2007, Saab et al. 2009, Wightman et al. 2010,

Saracco et al. 2011, Latif et al. 2013, Tingley et al. 2016). The availability of habitat suitability models is relatively limited, however, in the Sierra Nevada and Southern Cascades of California (hereafter, Sierra Nevada), a forested region of great interest for management and species conservation with unique tree species composition, predator communities, and fire regimes that may influence woodpecker behavior in ways that limit applicability of habitat suitability models developed in other regions. Published models appropriate for informing post-fire management of woodpecker habitat in the Sierra Nevada are currently limited to a single species, the Black-backed Woodpecker (*Picoides arcticus*; Saracco et al. 2011, Seavy et al. 2012, Tingley et al. 2016, Stillman et al. 2019a). Tingley et al. (2016) provided a robust hierarchical model developed from space-use and occupancy data that predicts Black-backed Woodpecker density across recently burned areas, but the model lacks information on the location and characteristics of their nest sites. Others have quantified Black-backed Woodpecker nesting habitat, but did not explicitly predict nesting distributions at new locations (Seavy et al. 2012, Stillman et al. 2019a).

We developed nest-site habitat suitability models using nest locations of 4 woodpecker species—Black-backed Woodpecker, Hairy Woodpecker (*Dryobates villosus*), White-headed Woodpecker (*D. albolarvatus*), and Northern Flicker (*Colaptes auratus*)—from 3 recent wildfires in the Sierra Nevada to inform post-fire management. We developed models that compared nest vs. non-nest sites for each species using (1) exclusively remotely sensed covariates to support habitat mapping, and (2) combinations of remotely sensed and field-collected covariates to inform fine-scale management prescriptions. We emphasized predictive performance across wildfire locations when selecting models to retain relationships with broad applicability for informing management in newly burned locations.

METHODS

Study Locations

We studied nesting woodpeckers in 3 wildfire locations on the Lassen and Plumas National Forests at the intersection of the Sierra Nevada and Southern Cascade mountain ranges (hereafter, Northern Sierra Nevada) in northeastern California (Figure 1, Table 1). The Moonlight Fire (40.233°N, 120.750°W) burned in September, 2007; the Cub Fire (40.183°N, 121.467°W) burned in June and July, 2008; and the Chips Fire (40.083°N, 121.183°W) burned in August and September, 2012 (hereafter Moonlight, Cub, and Chips, respectively). In Chips we excluded the 10,246 ha of the 2000 Storrie Fire that overlapped the Chips fire footprint, and, due to funding

source constraints, all of Plumas National Forest (Figure 1). Moonlight, Cub, and Chips footprints contained 27%, 12%, and 12% private lands, respectively. Our surveys covered an elevation range of 1,126–1,998 m (mean: 1,658 m) at Moonlight, 1,199–2,190 m (mean: 1,779 m) at Cub, and 1,438–1,896 m at Chips (mean: 1,663 m). Spacing among perimeters of the 3 locations ranged from 10 to 48 km. Using the U.S. Forest Service vegetation burn severity data, 56% of Moonlight was high-severity burn (>75% canopy mortality), 27% was moderate (25–75% canopy mortality), and 17% was low or unchanged (<25% canopy mortality); 20% of Cub was high severity, 31% was moderate, and 49% was low or unchanged; and 22% of Chips was high severity, 35% moderate, and 43% low or unchanged (USDA 2017). Before wildfire, our study area included dry mixed-conifer forest, moist mixed-conifer forest, and fir-dominated forest (*Abies* spp.) distributed from lower to higher elevations, respectively, with small amounts of montane chaparral interspersed throughout. Common tree species included yellow pine (*Pinus ponderosa* and *P. jeffreyi*), sugar pine (*P. lambertiana*), red fir (*Abies magnifica*), white fir (*A. concolor*), lodgepole pine (*P. contorta*), and Douglas fir (*Pseudotsuga menziesii*). Like much of the Sierra Nevada after Euro-American settlement, our study area was subject to intensive timber harvest before the 1990s, focusing mostly on large trees >60 cm DBH (i.e. diameter at breast height), and a century of fire suppression (Fites-Kaufman et al. 2007). Consequently, our study area had experienced structural homogenization and was dominated by second-growth, high densities of small and medium sized trees, and dense canopy cover (Fites-Kaufman et al. 2007).

Nest and Non-nest Locations

We searched for active nest cavities along 45 20-ha belt transects (0.2 × 1 km rectangle) on U.S. Forest Service land across the 3 wildfire locations 1–5 yr post-fire (Table 1). We placed belt transects by generating random points with a minimum spacing of 1.5 km, from which transects were oriented at a random bearing. To allow safe navigation, we limited sampling to areas with a slope of <40%. We also dropped one randomly selected belt transect in Cub that occurred in entirely non-forested chaparral habitat before the fire. Transects were initially located in ArcMap 9.2 and 10.1 (ESRI 2012). We searched each transect annually between May 14 and July 5, the nesting season for woodpeckers in our study area, following established protocols (Dudley and Saab 2003). We surveyed each belt transect twice each nesting season with 8–21 days between visits. We began surveys 1–2 hr after sunrise and ended by noon. Surveyors meandered through belt transects, looked for individual woodpeckers, and followed them back to their cavities, paying particular attention
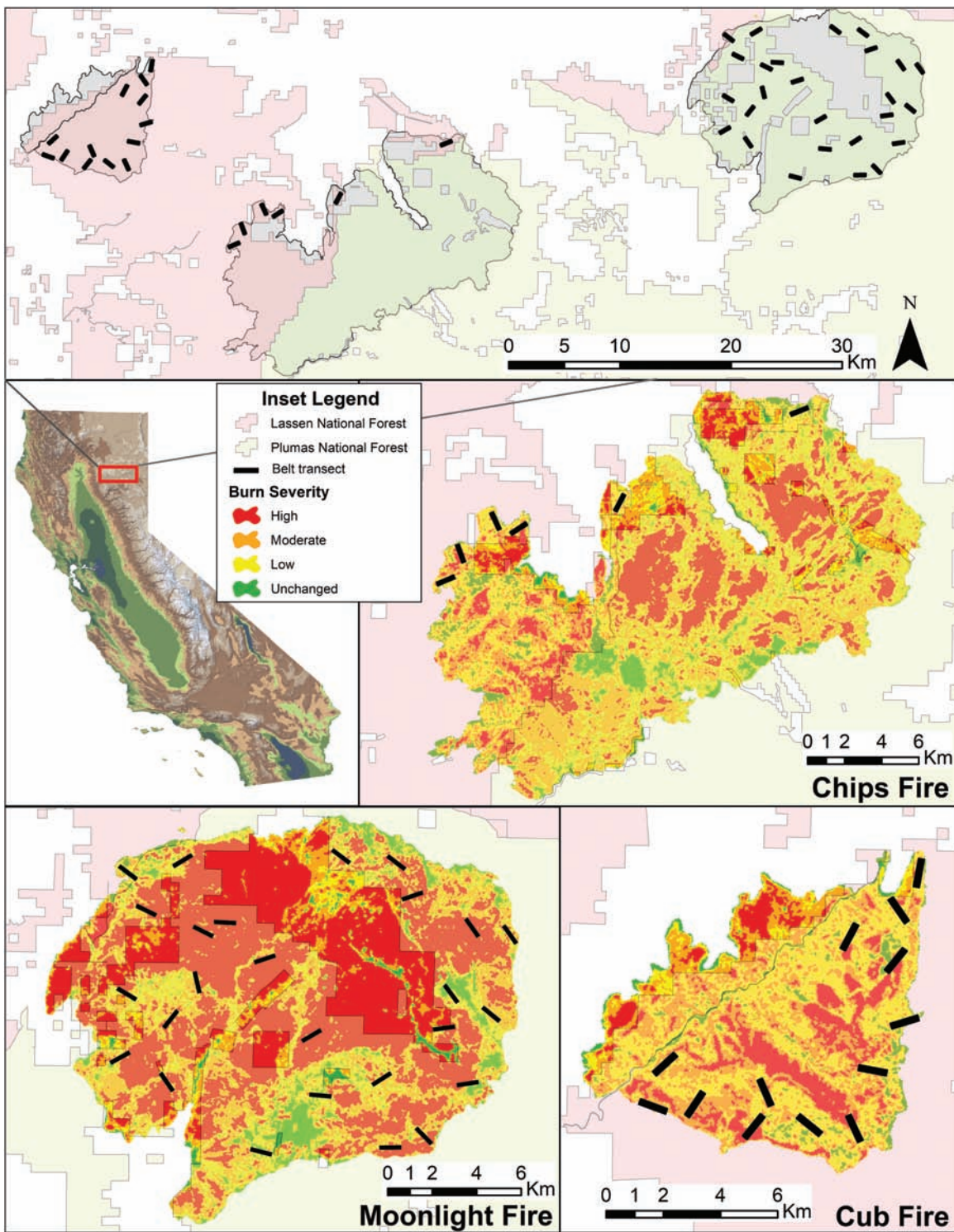
FIGURE 1. Sampling locations at 3 wildfire study locations where habitat suitability models were developed and evaluated in the Northern Sierra Nevada Mountains (California, USA). Transparent pink and green polygons indicate boundaries of Lassen and Plumas National Forests, respectively.

to individuals exhibiting breeding behaviors (Martin and Geupel 1993). A nest was considered occupied when we observed adults entering and remaining in the cavity for >10 min, heard young begging within the cavity, or observed adults carrying food into the cavity. We primarily searched within transect boundaries, but located 36% of

nests ≤397 m (2% > 200 m) outside transect boundaries when following birds initially detected within transect boundaries.

For non-nest sites, we generated coordinates for 5 random points in each belt transect using ArcMap 9.2 and 10.1 (ESRI 2012) each survey year. We navigated to these coordinates in the field using a handheld GPS unit. Once within 10 m of a point's coordinates, we located the nearest snag or live tree >12 cm DBH (minimum size of any woodpecker nest tree in the first study year) and centered all non-nest measurements at this tree.

Environmental Data

We compiled remotely sensed data at a 30 × 30 m resolution to describe topography, burn severity, and pre-fire forest structure and composition (Tables 2 and 3). We summarized variables at 3 scales centered on nest and non-nest sites: an individual pixel scale (0.09 ha; slope, aspect), a local scale (3 × 3 pixels, 0.81 ha; burn severity, canopy cover, and dominant tree size), and a landscape scale (1-km-radius circle, 314 ha; burn severity, canopy cover, dominant tree size, percent true fir forest). Variables at pixel and local scales represented conditions near the

TABLE 1. Sampling and timing of wildfires at 3 study locations where habitat suitability models were developed and evaluated in the Northern Sierra Nevada Mountains (California, USA). Models were developed for nesting Black-backed Woodpecker (BBWO), Hairy Woodpecker (HAWO), White-headed Woodpecker (WHWO), and Northern Flicker (NOFL).

| | Timing | | Spatial extent (ha) | | | n | |
| | Ignition | Sampling | Full | Surveyed (no. belt transects) | Nesting species | nest | non-nest |
Fire							
Moonlight	2007	2009–2012	26,403	858 (26)	BBWO	24	337
					HAWO	46	274
					WHWO	30	325
					NOFL	29	315
Cub	2008	2009–2012	6,169	428 (13)	BBWO	19	100
					HAWO	27	79
					WHWO	20	112
					NOFL	17	98
Chips	2012	2013–2016	31,114	197 (6)	BBWO	28	41
					HAWO	24	40
					WHWO	38	45
					NOFL	11	68

TABLE 2. Remotely measured habitat features and variables considered in nest habitat models for woodpeckers after wildfire. k is the number of variables used to represent a listed habitat feature. All data were initially retrieved at a 30-m pixel resolution (0.09 ha), and some were smoothed using 0.81- or 314-ha moving-window neighborhoods. Data sources were LANDFIRE (2017) for topography, U.S. Forest Service Rapid Assessment of Vegetation Condition after Wildfire (RAVG) for burn severity, and California Wildlife Habitat Relationships (CWHR) habitat classifications within U.S. Forest Service CALVEG data layers for pre-fire forest structure and composition.

Feature (variable[s])	k	Scale(s)	Description
Slope (SLOPE)	1	0.09 ha	Pixel topographic slope as % rise over run
Aspect (SASP + CASP)	2	0.09 ha	Sine- (east–west) + cosine-transformed (north–south) pixel orientation of topographic slope
Local burn severity (LocBurn)	1	0.81 ha	Median percent canopy mortality (RdNBR-derived) [a] for 3 × 3 pixel neighborhood
Landscape burn severity (LandBurn)	1	314 ha	Percent of 1-km radius neighborhood with >64% canopy mortality (RdNBR-derived) [a]
Pre-fire canopy cover (LocCC, LandCC)	2	0.81 or 314 ha	Percent of 3 × 3 pixel (0.81 ha) or 1-km radius (314 ha) neighborhood with >40% canopy cover before wildfire [b]
Pre-fire tree size dominance (LocSizeSm, LandSizeSm, LocSizeLrg, LandSizeLrg)	4	0.81 or 314 ha	Percent of 3 × 3 pixel (0.81 ha) or 1-km radius (314 ha) neighborhood dominated by small trees (DBH = 28–61 cm) or by large trees (DBH > 61 cm) before wildfire [c]
Pre-fire fir dominance (LandFir)	1	314 ha	Percent of 1-km-radius (314 ha) neighborhood dominated by true fir [d]
Logging (LandLog) [e]	NA	314 ha	Proportion area treated with salvage logging

[a] Equivalent to RdNBR (Relativized delta Normalized Burn Ratio) > 548, which falls within the moderate burn severity category defined by Miller and Thode (2007).
[b] >40% pre-fire canopy cover was represented as CWHR Density classes M or D.
[c] Small- and large-tree dominated pixels were CWHR Size codes 4 and 5, respectively.
[d] Fir dominance was represented as CWHR types red fir or white fir.
[e] Logging variables were not considered as model covariates, but were summarized to inform discussion.

TABLE 3. Field-measured habitat features and variables considered in nest habitat models for woodpeckers after wildfire. *k* is the number of variables that represented a listed habitat feature. Variables measured at the tree scale quantify nest trees or center trees for non-nest sites.

Feature (variable[s])	*k*	Scale(s)	Description
Snag density by size class (SnagDens23to50, SnagDensGT50, SnagDensGT23)	3	0.04 ha	Number of snags with DBH of specified size (23–50 cm, >50 cm, or >23 cm) within 11.3 m radius circle.
Snag density by species (PineDens, FirDens)	2	0.04 ha	Number of pine (*Pinus* spp.) or fir (*Abies* spp. and *Pseudotsuga menziesii*) snags within 11.3-m-radius circle.
Tree diameter (DBH) [a]	1	tree	Diameter at breast height (1.4 m)
Tree species (TreeSpPine, TreeSpFir) [b]	2	tree	Species (*Pinus* spp. or *Abies* spp.)
Broken top (BRKN)	1	tree	Top condition (0 = intact, 1 = broken)
Time since fire (TimeSincFire) [b]	1	annual	Number of years since wildfire ignition year

[a] Linear and quadratic relationships were considered for DBH.
[b] In addition to linear relationships with Tree species, we considered interactive effects of Tree species and Time since fire (e.g., TreeSpPine + TimeSincFire + TreeSpPine * TimeSincFire). Time since fire was only considered as an interactor and never alone.

nest, whereas landscape-scale variables represented conditions over an area where foraging decisions could be made, which is an area in which a home range could be contained relative to a nest location (Garrett et al. 1996, Tingley et al. 2014). We derived topographic variables from digital elevation model layers (LANDFIRE 2017). We used canopy mortality data from the U.S. Forest Service Rapid Assessment of Vegetation Condition after Wildfire (RAVG) data products for burn severity variables, which are derived from a change detection algorithm, the Relative Differenced Normalized Burn Ratio, that uses 2 Landsat Thematic Mapper images captured before and after a wildfire (Miller and Thode 2007). RAVG data may underrepresent tree mortality compared to other burn severity data (i.e. MTBS 2018), but they are immediately available after wildfire and therefore frequently used to inform post-fire planning. We derived pre-fire canopy cover, dominant tree size, and forest type based on tree species dominance from U.S. Forest Service CALVEG data layers (USDA 2004). We used proportion of true fir forest as a covariate rather than elevation or climatic variables because tree species dominance depends on these factors and is more directly relevant to woodpecker ecology.

Field-collected data included information on snag/tree species, density, DBH, and tree-top condition associated with nest and non-nest sites (Table 3). Our study species are known to strongly favor standing dead wood for cavity excavation. Accordingly, nest cavities favored snags but also occurred in live trees, presumably often where portions had died. We did not record whether any portions of live trees at non-nest sites were dead, nor did we restrict non-nest sites to trees that were at least partially dead. Therefore, we instead randomly reduced live-tree non-nest sites to match the proportion of nests centered on snags (97%, 99%, 92%, and 98% for Black-backed Woodpecker, Hairy Woodpecker, White-headed Woodpecker, and Northern Flicker, respectively), thus approximating the selection for nests in standing dead wood. We recorded

DBH, species, tree-top condition, and counts for all snags >23 cm in an 11.3-m-radius plot centered on nest and non-nest snags/trees to inform patch-scale (0.04 ha) covariates (e.g., Raphael and White 1984, Russell et al. 2007; Table 3). We compiled 3 variables of snag density by size class, >23 cm, 23–50 cm, and >50 cm, for analysis (Table 3). We chose these DBH categories for density data because of their relevance to management of U.S. Forest Service lands (Marcot et al. 2010). We lumped snag/tree species into 3 categories: fir (*A. concolor*, *A. magnifica*, and *Pseudotsuga menziesii*), pine (*Pinus* sp.), and other species (Table 3). Fir and pine groupings each included species that could not always be readily distinguished from each other when dead and heavily scorched. The other species category included less common trees and severely decayed snags not identifiable to species.

We did not model relationships with salvage logging to avoid over-fitting to surveyed conditions at any one location; however, to better describe the range of conditions under which our models were built and guide future model applications, we used the U.S. Forest Service Region 5 Forest Activities database (USDA 2016) and U.S. Forest Service land ownership boundaries to estimate extent of salvage logging at the 3 locations. Salvage logging affected 3%, 28%, and 31% of the landscape within 1 km of random sites at Cub, Chips, and Moonlight, respectively. These estimates of logging extent overrepresented amount treated because treatment polygons included some untreated areas and did not reflect treatment intensity. Salvage logging treatments within polygons were highly variable in extent and intensity depending on tree size, burn severity, and proximity to roads, ranging from clearcuts in high-severity burned areas on most private lands, 10% snag retention in high-severity burned areas on public land, to no harvest where roadside units overlapped low-severity burned areas. Nevertheless, these data represented the best available information and were useful for comparison of logging across locations. Logging extent was highest

in Moonlight, where private lands were most extensive. Seven of 26 transects in Moonlight intersected public land salvage units, of which 19–96% (mean = 45%) overlapped salvage units. In contrast, Chips and Cub transects did not overlap salvage units.

Habitat Suitability Index Models

We used weighted logistic regression contrasting environmental conditions at nest vs. non-nest sites to generate HSIs. We weighted observations of zeros (non-nest) and ones (nest) according to their relative sample sizes ($w_1 = 1$; $w_0 = n_1/n_0$; Russell et al. 2007, Saab et al. 2009). This weighting scheme treats the ratio of zeros to ones as an artifact of sampling with no biological significance. Thus, weighting ensured estimated response probabilities ranged from 0 to 1, readily interpretable as an index of suitability, and that observations of 0s and 1s informed model parameter estimates equally, reflecting our case–control sampling design (Russell et al. 2007). Ideally, zeros in the data should represent unused sites not contaminated with misclassified nest sites (Keating and Cherry 2004). Our field methods resulted in a thorough search within belt-transect boundaries, so we are reasonably confident that non-nest sites were not used for nesting during study years. Additionally, we excluded non-nest sites within 130 m of any known nest sites for a given focal species to ensure that 3×3 cell neighborhoods for non-nest sites would not overlap those for any nest sites. We fitted weighted logistic regression models using the *glm* function in R v. 3 (R Core Team 2016; code available at https://doi.org/10.5281/zenodo.3354378). Some figures were generated using *ggplot* 2 (Wickham 2016).

With an emphasis on identifying simple, predictive models to guide management, we constructed candidate models that exhausted potential covariate combinations while restricting model complexity based on sample size (see also Russell et al. 2007, Latif et al. 2016). We limited the number of covariates in a model to ≤1/10th the number of nests in the analyzed sample rounded down. We *z*-scored (mean = 0, SD = 1) all covariates prior to modeling. We prohibited covariate pairs with Pearson's $|r| \geq 0.7$ to avoid multicollinearity (Kutner et al. 2004). We primarily considered linear covariate relationships but also considered second-order (quadratic or interactive) relationships where a clear ecological basis existed (i.e. quadratic relationships with DBH and interactions of nest tree species with time since fire). The quadratic relationship with DBH reflects potential selection for mid-sized trees (Seavy et al. 2012, Stillman et al. 2019a). The interaction of nest tree species with time since fire reflects a potential switch in nest tree selection owing to the differential decay rates of fir and pine species (Forristal 2009, Ritchie et al. 2013). We constructed candidate models restricted to remotely sensed covariates (hereafter remote-sensing models) and models that included both remotely sensed and field-collected covariates (combination models).

We emphasized predictive performance for selecting models while also excluding the poorest-performing models with respect to relative fit and parsimony (Table 4). We quantified predictive performance using spatial cross-validation, wherein we withheld data from one wildfire at a time, fit each candidate model to remaining data, and calculated a Resource Selection Function Plot Index (RPI) for withheld data (Wiens et al. 2008). Each RPI consisted of a Spearman's correlation coefficient (range: –1 to 1) relating average HSI with the observed proportion of nests for 10 equal-*n* moving-window bins (Appendix A). We excluded models with an RPI < 0.564 (critical value for $n = 10$

TABLE 4. Selection criteria for habitat suitability models for nesting woodpeckers in burned forests of Northern Sierra Nevada.

Criterion	Description	How applied
RPI	Mean Spearman's correlation coefficient (–1 to 1 range; $n = 3$ wildfires) relating observations with model predictions for each wildfire when withheld from model fitting via spatial cross validation	Models with RPI < critical value (0.564 for $n = 10$ and $\alpha = 0.05$) at any one wildfire were excluded. The model with highest mean RPI ($n = 3$ wildfires) that met all other criteria was selected.
ΔAIC_i	Akaike's information criterion for the *i*th model minus that of the top model (lowest AIC) of models fitted to data all 3 wildfire locations.	Models $\Delta AIC_i > 6$ were excluded. [a]
Sensitivity	Proportion nests classified suitable at any given wildfire using an optimized classification threshold, that is maximizes sensitivity (proportion nests suitable) + specificity (proportion non-nests unsuitable) (maxSSS threshold)	Models classifying <0.5 of nest sites suitable at any one wildfire using the maxSSS threshold were excluded.
Parsimony	Statistical support for model coefficients based on *z*-statistic	Models with statistically unsupported coefficients ($P > 0.05$) [b] were excluded. [c]

[a] Corresponds to model weight of 95%.
[b] When none met this criterion, we relaxed the required statistical support to $P \leq 0.1$ for any coefficient.
[c] For second-order relationships (quadratic or interactive), only statistical support for the highest-order parameter was considered when assessing parsimony. Exclusion of models with weakly supported coefficients follows Wiens et al. (2008).

and α = 0.05) at any location (Wiens et al. 2008). We also excluded models with ΔAIC > 6 (relative fit corrected for parsimony; Burnham and Anderson 2002); models that did not reliably classify nests as suitable; and models with weakly supported coefficients (Table 4). Of remaining models, we retained the one with highest mean RPI ($n = 3$ wildfires) to inform management, although we also consider other high-performing models to identify important habitat relationships. If multiple top-ranked models had equivalent RPIs (within 0.01), we selected the one with the lowest AIC. For each species, we selected one remotely sensed model and one combination model. The number of candidate models ranged from 15 to 362 for each species after excluding those with RPI < 0.564. The large number of candidate models potentially give rise to concerns over data dredging. However, we avoided the pitfalls of data dredging (i.e. primarily model overfitting) by constraining covariates to a set of environmental features with clear relevance to species ecology, constraining model complexity (i.e. number of covariates) based on sample size, and emphasizing predictive performance when selecting models. Variation in the number of candidate models among model sets reflects (1) differences in sample size among species and consequent differences in the maximum number of covariates allowed in any candidate model, (2) differences in the number of potential covariates depending on whether field-collected covariates were considered, and (3) the number of models excluded due to low predictive performance (i.e. RPI < 0.564).

To aid interpretation of selected models, we related HSIs with observed nest densities and identified threshold values of HSIs useful for classifying low-, moderate-, and high-suitability habitat. We first plotted densities for equal-n moving-window bins to examine relatively continuous changes in density along HSI gradients, and then identified thresholds distinguishing suitability categories associated with different densities (Hirzel et al. 2006). In contrast with moving-window bins for calculating RPIs assessed at individual locations (see Appendix A), we plotted densities for >10 bins to facilitate visual evaluation of the data across all wildfire locations. Finally, we calculated 95% confidence intervals (CIs) for class-specific densities using nonparametric bootstrapping (Efron and Tibshirani 1986), which helped us verify the distinctness of suitability classes. We bootstrapped CIs at the transect level ($n = 45$ transects), wherein we assigned transect IDs to the nearest nest and non-nest sites and then resampled the data by transect ID with replacement. We generated 5,000 bootstrapped samples and reported 2.5th and 97.5th median-unbiased percentiles for bootstrapped samples (calculated with *quantile* function in R with type = 8) as confidence limits. Observed nest densities were not corrected for detectability, but woodpecker nests in post-fire

areas are highly detectable with our survey methods, particularly after hatching (Russell et al. 2009) and 1–2 yr post-fire when woodchips excavated from nest cavities are often clearly visible below the nest tree, and survival rates are high (Saab et al. 2011). We therefore assumed low detectability bias and no habitat-related variation in this bias to infer relative change along HSI gradients from observed densities. We calculated similar densities when including vs. excluding nests <50 m outside transects, suggesting survey effort (and consequent detectability) was evenly distributed within this area. We therefore included nests inside and <50 m outside transects ($n = 54$, 90, 72, and 48 for Black-backed Woodpecker, Hairy Woodpecker, White-headed Woodpecker, and Northern Flicker, respectively; 84% of total sample) for calculating observed densities.

RESULTS

We monitored 71 nests of Black-backed Woodpecker, 97 nests of Hairy Woodpecker, 88 nests of White-headed Woodpecker, 57 nests of Northern Flicker, and 1,834 non-nest sites at 3 wildfire locations during years 2009–2016 (Appendix Tables 10 and 11). We observed notable differences in remotely sensed and field-measured environmental conditions at nest vs. non-nest sites, and differences among wildfire locations (Appendix Table 11). Nest sites for all 4 species were characterized by higher local-scale burn severity and higher snag densities compared to non-nest sites (Appendix Table 11). This difference, however, did not hold with landscape-scale burn severity (Appendix Table 11). Nest sites were characterized by gentler slopes and smaller-diameter trees (pre-fire) at both local and landscape scales compared to non-nest sites (Appendix Table 11). Nest cavities were also located in broken-top snags more frequently than available (Appendix Table 11). Topographic slope and pre-fire canopy cover were relatively low at Chips sites relative to other locations (Appendix Table 11). Larger trees tended to dominate Moonlight sites and smaller trees dominated Chips sites, with Cub being intermediate (Appendix Table 11). True fir dominated Chips sites more so than at the other locations (Appendix Table 11).

Remote-Sensing Models
We identified remote-sensing models that performed well (RPI ≥ 0.968) and met all minimum requirements for model selection for Black-backed, Hairy, and White-headed woodpeckers (Table 5). For Northern Flicker, no model met all minimum requirements, so we relaxed the parsimony requirement (i.e. allowed models with marginally supported coefficients at $0.1 > P \geq 0.05$). The top-ranked model for Northern Flicker did not perform as well

as selected models for other species, but was still informative (RPI = 0.836).

All remotely sensed HSI models that met our minimum requirements included a local-scale positive relationship with burn severity (Tables 5, 6 and Appendix Figures 5–8). Models for Black-backed and White-headed woodpecker also described negative relationships with landscape-scale burn severity (Tables 5, 6 and Appendix Figures 5, 7). Black-backed and Hairy woodpecker exhibited positive relationships with pre-fire canopy cover, with the local scale

being more important for Black-backed Woodpecker, and the landscape scale for Hairy Woodpecker (Tables 5, 6 and Appendix Figures 5, 6). Selected models for Hairy Woodpecker and Northern Flicker described negative relationships with local-scale proportion area dominated by large trees (Table 6 and Appendix Figures 6, 8). Although not appearing in the top model, negative relationships with large-tree dominance or positive with small-tree dominance were supported in other predictive models for Black-backed Woodpecker (Table 5). The Northern Flicker model also

TABLE 5. Model selection results with only remotely sensed covariates. Models quantify nesting habitat for Black-backed Woodpecker (BBWO), Hairy Woodpecker (HAWO), White-headed Woodpecker (WHWO), and Northern Flicker (NOFL) after wildfire. Parameters describing covariate relationships and their sign (+/−) are listed for each model. For variable descriptions, see Table 1. RPI = mean Spearman's rank correlation relating observed data with model predictions for data withheld during model fitting via cross validation. ΔAIC_i = the difference in AIC for the ith model vs. the top-ranked (lowest AIC) model in a given set. Sensitivity is the minimum proportion of nest sites classified suitable (of 3 wildfire locations) using the HSI threshold that maximizes sensitivity plus specificity (proportion non-nest sites classified unsuitable; maxSSS threshold). Listed models are those meeting minimum requirements for RPI, ΔAIC_i, Sensitivity, and parsimony (described in Table 3).

Species	Model covariate relationships (direction of relationships)	RPI (SD)	ΔAIC_i	Sensitivity (maxSSS threshold)
BBWO	LocBurn (+), LandBurn (−), LocCC (+) [a]	0.968 (0.010)	2.71	0.63 (0.41)
	LocBurn (+), LandBurn (−), LocCC (+), LocSizeLrg (−)	0.935 (0.046)	1.07	0.75 (0.37)
	LocBurn (+), LandBurn (−), LocCC (+), LandSizeLrg (+)	0.882 (0.128)	0.45	0.63 (0.44)
	LocBurn (+), LandBurn (−)	0.858 (0.109)	4.16	0.75 (0.35)
	LocBurn (+), LocCC (+), LandSizeSm (+)	0.844 (0.150)	4.98	0.53 (0.48)
	LocBurn (+), LandBurn (−), LocCC (+), LocSizeSm (+)	0.839 (0.195)	2.33	0.71 (0.38)
	LocBurn (+), LandBurn (−), LandSizeSm (+)	0.790 (0.196)	1.59	0.67 (0.44)
	LocBurn (+), LandBurn (−), LocCC (+), LandSizeLrg (−)	0.752 (0.216)	0.00	0.71 (0.42)
HAWO	LocBurn (+), LandCC (+), LocSizeLrg (−) [a]	0.990 (0.005)	2.71	0.56 (0.51)
	LocBurn (+), LandSizeSm (+)	0.956 (0.035)	0.09	0.67 (0.46)
	LocBurn (+), LandCC (+), LandSizeLrg (−)	0.944 (0.026)	2.04	0.67 (0.46)
	LocBurn (+), LocSizeLrg (−)	0.769 (0.150)	3.98	0.56 (0.52)
WHWO	LocBurn (+), LandBurn (−) [a]	0.977 (0.009)	0.00	0.53 (0.49)
NOFL	SLOPE (−), LocBurn (+) [b], LocSizeLrg (−), LandSizeLrg (+) [a,b]	0.836 (0.119)	0.76	0.59 (0.46)
	SLOPE (−), LocBurn (+), LocSizeLrg (−) [b]	0.772 (0.167)	0.00	0.65 (0.44)

[a] Selected models are those that maximize RPI of listed candidates.
[b] Coefficients with $0.1 > P \geq 0.05$ for z statistic testing for deviation from zero. All other coefficients were statistically supported with $P < 0.05$.

TABLE 6. Parameter estimates (and SEs) for selected habitat suitability (weighted logistic regression) models with remotely sensed covariates for nesting woodpeckers in Northern Sierra Nevada burned forests. Nesting species are Black-backed Woodpecker (BBWO), Hairy Woodpecker (HAWO), White-headed Woodpecker (WHWO), and Northern Flicker (NOFL). Variable descriptions are in Tables 2 and 3.

Parameter	BBWO	HAWO	WHWO	NOFL
Intercept	−0.86 (0.26)	−0.48 (0.19)	−0.56 (0.2)	−0.33 (0.23)
LocBurn	1.73 (0.34)**	0.89 (0.18)**	1.5 (0.29)**	0.39 (0.22)*
LandBurn	−1.62 (0.32)**	−	−1.82 (0.3)**	−
LocCC	0.82 (0.35)**	−	−	−
LandCC	−	0.4 (0.17)**	−	−
LocSizeLrg	−	−0.47 (0.17)**	−	−0.65 (0.27)**
LandSizeLrg	−	−	−	0.39 (0.23)*
SLOPE	−	−	−	−0.57 (0.26)**

*$P \leq 0.1$ based on z-test for difference from zero (not applied to Intercept).
**$P \leq 0.05$ based on z-test for difference from zero (not applied to Intercept).

described a negative relationship with topographic slope and a marginally supported positive relationship with landscape-scale large tree dominance (Table 6 and Appendix Figure 8).

Combination Models

We identified combination models for all 4 species that performed well and met minimum requirements for selection (Table 7). Two top-ranked models for Black-backed Woodpecker exhibited equivalent predictive performance, so we selected the one with lower AIC. The 2 top-ranked models for White-headed Woodpecker and Northern Flicker also exhibited very similar predictive performance relative to the RPI SD. In both cases we chose the model with slightly higher predictive performance and lower AIC. Predictive performance for the selected Northern Flicker model was lower than for other species, but nevertheless strong (RPI = 0.935), and notably stronger than the remotely sensed model for this species (see above, Table 5).

Selected combination models for the Black-backed, Hairy, and White-headed woodpeckers mirrored remote-sensing models as all described positive relationships with local-scale burn severity; Black-backed and White-headed woodpecker models described negative relationships with landscape-scale burn severity; and the Hairy Woodpecker model described a negative relationship with local-scale dominance of large trees (Table 8 and Appendix Figures 9–11). The selected combination model for Northern Flicker contained no remotely sensed covariates (Table 8 and Appendix Figure 12), although supported relationships with remotely sensed covariates appeared in other models (i.e. positive with burn severity, negative with slope, and negative with local-scale large tree-size dominance; Table 7). Selected combination models also described strongly supported relationships with diameter and top condition of the nest tree (Tables 7, 8). For Black-backed Woodpecker, White-headed Woodpecker, and Northern Flicker models, HSIs peaked at DBH values of 44, 92, and 86 cm, respectively (Appendix Figures 9, 11, 12). Hairy Woodpecker, White-headed Woodpecker, and Northern Flicker models described affinities for broken-top snags (Table 8 and Appendix Figures 10–12). Additionally, Hairy Woodpecker HSIs related positively with nest tree DBH (Table 8 and Appendix Figure 10). Although not appearing in selected models, positive relationships with snag density within the nest patch were supported in other strongly predictive models for Black-backed and Hairy woodpeckers (Table 7). A positive relationship with pine as the nest tree species with increasing time since fire was also supported in other predictive models for Hairy Woodpecker (Table 7).

HSI Categories and Nest Density

Observed nest densities generally increased along HSI gradients but also revealed some breaks and fluctuations in this relationship (Figures 2, 3). For remote-sensing models, observed nest densities for all species clearly differed among the 3 suitability categories (low, moderate, and high; Figure 2). For combination models, we also identified 3 suitability categories that differentiated observed densities for Black-backed, Hairy, and White-headed woodpeckers (Figure 3). For the Northern Flicker combination model, however, nest HSIs (mean = 0.79) differed too much from non-nest HSIs (mean = 0.18) to identify 3 suitability categories, so we only identified 2 (Figure 3). For most models, high-suitability areas contained much higher nest densities than areas classified low or moderate, whereas low- and moderate-suitability areas differed less from each other; this pattern was especially evident in the combination models.

DISCUSSION

We identified models for all 4 species with strong predictive performance across wildfire locations despite notable variation in conditions among locations, suggesting broad applicability to guide post-fire management in the Northern Sierra Nevada. Relationships appearing in selected models along with other strongly predictive models add to our understanding of species' ecological relationships. Positive relationships with local-scale burn severity were consistent with the disturbance-related ecology of our study species (e.g., Russell et al. 2007, Latif et al. 2013). Some relationships, however, may be specific to the Sierra Nevada or potentially even just the Northern Sierra Nevada (e.g., a negative relationship with landscape-scale burn severity for Black-backed Woodpecker), highlighting the importance of region-specific studies. Models restricted to remotely sensed covariates exhibited similar predictive performance as combination models. Thus, we provide tools with apparent applicability both for mapping nest-site habitat across wildfire locations and for informing fine-scale management prescriptions.

How Modeled Relationships Reflect Species Ecology

Relationships appearing in selected and strongly predictive models are largely consistent with current knowledge of nesting ecology for our study species. Positive relationships with local-scale burn severity (remotely sensed) for the 4 species were consistent with other studies (Russell et al. 2007, Saab et al. 2009, Wightman et al. 2010, Latif et al. 2013).

Relationships for Hairy Woodpecker with large, broken-top (i.e. decayed) nest snags in higher-severity burned sites within landscapes dominated by smaller trees and high pre-fire canopy cover were consistent with patterns reported by others (Russell et al. 2007, Vierling et al. 2008, Saab et al. 2009). High pre-fire canopy cover likely indexes high snag densities with foraging opportunities for saproxylic insect

TABLE 7. Model selection results with remotely sensed and field-collected covariates. Models quantify nesting habitat for Black-backed Woodpecker (BBWO), Hairy Woodpecker (HAWO), White-headed Woodpecker (WHWO), and Northern Flicker (NOFL) after wildfire. Parameters describing covariate relationships and their sign (+/−) are listed for each model. For variable descriptions, see Tables 1 and 2. RPI = mean Spearman's rank correlation relating observed data with model predictions for data withheld during model fitting via cross validation. ΔAIC_i = the difference in AIC for the ith model vs. the top-ranked (lowest AIC) model in a given set. Sensitivity is the minimum proportion of nest sites classified suitable (of 3 wildfire locations) using the HSI threshold that maximizes sensitivity plus specificity (proportion non-nest sites classified unsuitable; maxSSS threshold). Listed models are those meeting minimum requirements for RPI, ΔAIC_i, Sensitivity, and parsimony (described in Table 3).

Species	Model covariate relationships (direction of relationships)	RPI (SD)	ΔAIC_i	Sensitivity (maxSSS threshold)
BBWO	LocBurn (+), LandBurn (−), DBH (+), DBH^2 (−)	0.994 (0.008)	2.18	0.71 (0.47)
	LocBurn (+), LandBurn (−), LocCC (+), DBH (+), DBH^2 (−) [a]	0.993 (0.005)	1.33	0.67 (0.49)
	LocBurn (+), LandBurn (−), LocCC (+), DBH (+), DBH^2 (−), SnagDens23to50 (+)	0.970 (0.046)	0.00	0.67 (0.51)
	LocBurn (+), LandBurn (−), DBH (+), DBH^2 (−), SnagDens23to50 (+)	0.952 (0.039)	0.44	0.71 (0.47)
	LocBurn (+), LandBurn (−), LocCC (+), SnagDens23to50 (+)	0.939 (0.047)	5.53	0.63 (0.42)
HAWO	LocBurn (+), LocSizeLrg (−), DBH (+), BRKN (+) [a]	0.996 (0.004)	5.69	0.7 (0.41)
	LocBurn (+), DBH (+), BRKN (+)	0.990 (0.013)	5.83	0.56 (0.49)
	LocBurn (+), LandCC (+), LocSizeLrg (−), DBH (+), BRKN (+)	0.989 (0.005)	5.41	0.74 (0.44)
	LocBurn (+), LandCC (+), LocSizeLrg (−), DBH (+), DBH2 (−), BRKN (+)	0.985 (0.013)	1.81	0.67 (0.54)
	LocBurn (+), DBH (+), BRKN (+), SnagDensAll (+)	0.985 (0.021)	4.45	0.52 (0.52)
	LocBurn (+), DBH (+), DBH2 (−), BRKN (+)	0.982 (0.016)	1.12	0.78 (0.36)
	LocBurn (+), LocSizeLrg (−), DBH (+), BRKN (+), SnagDensAll (+)	0.979 (0.024)	3.82	0.67 (0.42)
	LocBurn (+), LandCC (+), LocSizeLrg (−), DBH (+), DBH2 (−), TreeSpPine (+), BRKN (+)	0.974 (0.025)	1.20	0.7 (0.53)
	LocBurn (+), LandCC (+), LocSizeLrg (−), BRKN (+), SnagDensAll (+), TreeSpPine (+), TimSinceFire (−), TreeSpPine * TimSinceFire (+)	0.973 (0.034)	3.84	0.75 (0.44)
	LocBurn (+), LandCC (+), LocSizeLrg (−), TreeSpPine (+), BRKN (+), SnagDensAll (+)	0.967 (0.041)	3.58	0.56 (0.57)
	LocBurn (+), DBH (+), DBH2 (−), SnagDensAll (+)	0.962 (0.019)	4.82	0.63 (0.47)
	LocBurn (+), LandCC (+), LocSizeLrg (−), BRKN (+), TreeSpPine (+), TimSinceFire (−), TreeSpPine * TimSinceFire (+)	0.957 (0.037)	5.92	0.54 (0.56)
	LocBurn (+), DBH (+), DBH2 (−), BRKN (+), TreeSpPine (+), TimSinceFire (−), TreeSpPine * TimSinceFire (+)	0.955 (0.054)	0.53	0.63 (0.54)
	LocBurn (+), LocSizeLrg (−), BRKN (+), SnagDensAll (+), TreeSpPine (+), TimSinceFire (−), TreeSpPine * TimSinceFire (+)	0.954 (0.025)	4.87	0.67 (0.42)
	LocBurn (+), LandCC (+), DBH (+), DBH2 (−), TreeSpPine (+), TimSinceFire (−), TreeSpPine * TimSinceFire (+)	0.951 (0.055)	5.73	0.67 (0.48)
	LocBurn (+), DBH (+), DBH2 (−), TreeSpPine (+), TimSinceFire (−), TreeSpPine * TimSinceFire (+)	0.945 (0.061)	5.80	0.67 (0.49)
	LocBurn (+), LandCC (+), LocTreeLrg (−), DBH (+), DBH2 (−), BRKN (+), TreeSpPine (+), TimSinceFire (−), TreeSpPine * TimSinceFire (+)	0.944 (0.070)	0.00	0.79 (0.41)
	LocBurn (+), LocSizeLrg (−), TreeSpPine (+), BRKN (+), SnagDensAll (+)	0.919 (0.105)	4.34	0.63 (0.46)
	LocBurn (+), LocSizeLrg (−), BRKN (+), SnagDensAll (+)	0.909 (0.123)	5.81	0.63 (0.52)
WHWO	LocBurn (+), LandBurn (−), DBH (+), DBH^2 (−), BRKN (+) [a]	0.985 (0.015)	0.00	0.63 (0.59)
	LocBurn (+), LandBurn (−), DBH (+), BRKN (+)	0.983 (0.015)	1.74	0.7 (0.61)
NOFL	DBH (+), DBH^2 (−), BRKN (+) [a]	0.935 (0.032)	1.14	0.82 (0.68)
	SLOPE (−), DBH (+), DBH^2 (−), BRKN (+)	0.930 (0.040)	1.22	0.82 (0.66)
	LocBurn (+), LocSizeLrg (−), DBH (+), DBH^2 (−), BRKN (+)	0.916 (0.049)	2.21	0.82 (0.56)
	LocSizeLrg (−), BRKN (+)	0.842 (0.116)	0.91	0.82 (0.13)
	BRKN (+)	0.796 (0.178)	1.80	0.82 (0.09)

[a] Selected models are those that maximize RPI of listed candidates.

TABLE 8. Parameter estimates (and SEs) for selected habitat suitability (weighted logistic regression) models with remotely sensed and field-collected covariates for nesting woodpecker in Northern Sierra Nevada burned forests. Nesting species are Black-backed Woodpecker (BBWO), Hairy Woodpecker (HAWO), White-headed Woodpecker (WHWO), and Northern Flicker (NOFL). Variable descriptions are in Tables 2 and 3.

Parameter	BBWO	HAWO	WHWO	NOFL
Intercept	−0.21 (0.3)	−1.01 (0.24)	−1.96 (0.38)	−2.34 (0.56)
LocBurn	1.63 (0.35)**	0.83 (0.19)**	1.65 (0.38)**	–
LandBurn	−1.53 (0.33)**	–	−1.81 (0.38)**	–
LocSizeLrg	–	−0.36 (0.17)**	–	–
DBH	0.95 (0.41)**	0.42 (0.2)**	1.28 (0.36)**	1.42 (0.58)**
DBH^2	−1.86 (0.58)**	–	−0.27 (0.12)**	−0.34 (0.17)**
BRKN	–	1.55 (0.35)**	2.66 (0.48)**	3.7 (0.65)**

**$P \leq 0.05$ based on z-test for difference from zero (not applied to Intercept).

prey (Saab et al. 2009). The importance of pine snags for nest cavity excavation is well established (e.g., Bull et al. 1997) while increasing use of pine with time since fire is less understood (Forristal 2009, Saab et al. 2009) and likely reflects species-specific decay patterns (Bull et al. 1997, Russell et al. 2006).

White-headed Woodpecker associations with large broken-top snags in higher-severity burned patches surrounded by lower-severity burned or unburned forest are consistent with patterns in southern Oregon (Wightman et al. 2010). Wildfire generates canopy openings and mosaics analogous to those favored for nesting by this species in unburned forest (Hollenbeck et al. 2011, Latif et al. 2015).

Modeled relationships of Black-backed Woodpeckers with (locally) high-severity burned patches and high snag densities (or pre-fire canopy cover indexing snag density) are consistent with other studies (Hutto and Gallo 2006, Russell et al. 2007, Saab et al. 2009, Seavy et al. 2012, Latif et al. 2016). Negative relationships with burn severity at the home range spatial scale, however, are unique to our study (see below). Although relationships with snag decay and tree species did not appear in strongly performing models for Black-backed Woodpeckers, these variables have been documented in our study region and elsewhere (Nappi and Drapeau 2011, Seavy et al. 2012, Tarbill et al. 2015); these features may be less important for predicting nesting distributions in the Northern Sierra Nevada.

For Northern Flicker, the selected model with field-collected covariates exclusively described relationships with nest tree characteristics. This model was consistent with other studies characterizing this species as a habitat generalist (Hutto and Gallo 2006, Russell et al. 2007, Saab et al. 2009). The Northern Flicker model restricted to remotely sensed covariates was informative, but contained some marginally supported covariate relationships and performance was weaker than for other species. We are least confident of the general utility of this model for predicting Northern Flicker post-fire nest-site habitat in the Northern Sierra Nevada.

Although they favored moderate- to high-severity burned patches locally, Black-backed Woodpeckers in our study sought these sites within landscapes characterized by lower-severity wildfire. While this pattern is inconsistent with those reported for Black-backed Woodpecker in burned forest elsewhere in their range, it is consistent with emerging evidence from the Sierra Nevada. In the northern Sierra Nevada, Black-backed Woodpeckers selected nest sites in high-severity burn patches, but closer to low-severity patches and unburned edges (Stillman et al. 2019a), possibly because fledglings select for medium- and low-severity burned forest where they received provisioning from adults (Stillman et al. 2019b). And in 2 large fires in the central and southern Sierra Nevada, Black-backed Woodpeckers were rarely detected in very large patches of high-severity fire (White et al. 2019). Greater extent of moderate- to high-severity wildfire in Sierra Nevada locations (Miller et al. 2009, Mallek et al. 2013, Steel et al. 2015) may encourage different selection patterns compared to other regions. Our study locations ranged 51–83% moderate- to high-severity, whereas other recently burned locations were reported to have a smaller range of affected area (e.g., 32–39%; Saab et al. 2007). Additionally, not all studies describe relationships with burn severity at multiple scales (e.g., Russell et al. 2007, Latif et al. 2013, Tingley et al. 2018). Although Black-backed Woodpeckers respond negatively to salvage logging (Hutto and Gallo 2006, Saab et al. 2007), and may have been negatively affected by salvage logging in our study locations, Black-backed Woodpecker relationships with burn severity in our study are likely not reflective of avoidance of logged units; the consistent relationships with landscape-scale burn severity and consistent positive relationship with local-scale severity across all 3 locations, despite substantial variation in salvage logging extent, support this conclusion, as do the recent findings of Stillman et al. (2019a, 2019b) and White et al. (2019).

Selection for nest sites within landscapes characterized by lower-severity wildfire may also be explained by
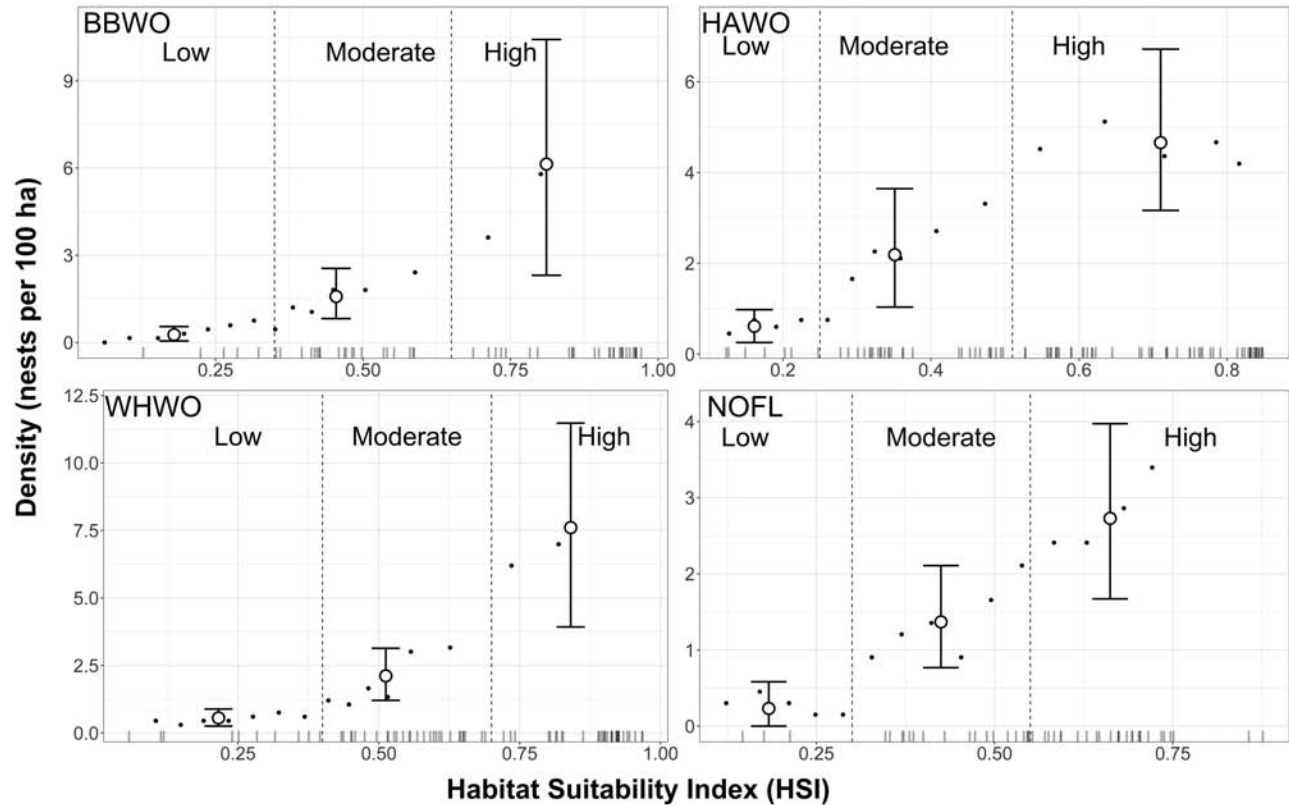
FIGURE 2. Nest densities plotted against HSI for equal-*n* moving-window bins (small black dots) and HSI-based suitability categories of low, moderate, and high (large open circles) for remote-sensing models. Data rugs represent nest sites.

dynamics in prey availability during the early years after fire. Foraging opportunities for woodpeckers are temporally constrained by the life cycles of their saproxylic insect prey (Nappi and Drapeau 2009). Trees die more rapidly in severely burned forest, and colonization by saproxylic insects is generally limited to the early stages of snag degradation during early post-fire years (Saint-Germain et al. 2004, 2007; Boulanger and Sirois 2007). In contrast, tree mortality in low- to moderate-severity burned stands may continue for longer (Angers et al. 2011, Woolley et al. 2012), potentially extending availability of foraging opportunities (Dudley and Saab 2007, Nappi et al. 2010). For example, extended foraging opportunities likely explains continued occurrence of Black-backed Woodpecker in lower-severity burned forests 6–8 yr after wildfire (Nappi et al. 2010, Dudley et al. 2012).

Model and Study Limitations
Although likely applicable beyond the Northern Sierra Nevada, models here are most applicable within the range of conditions where they were developed (Aarts et al. 2013, Bahn and McGill 2013), i.e. 1–5 yr post-fire in Sierra mixed conifer, white fir, and red fir forest types (Mayer and Laudenslayer 1988). These forest types are largely restricted

to the Sierra Nevada and Southern Cascades. Even within these forest types, the Sierra Nevada is characterized by strong north–south gradients in precipitation (greater north) and topographic relief (greater south), which influence burn severity patterns (Collins and Skinner 2014). Therefore, model evaluation with data from more southern locations of the Sierra Nevada would be desirable. We also expect poorer applicability to the dry pine-dominated forests on the lower elevation west and east sides of the Sierra Nevada and Southern Cascades. Such forests occurred at our study locations but represented only a small fraction of our surveyed area largely restricted to the eastern side of Moonlight. Model evaluation with more data from dry pine-dominated forest types is also desirable.

In our approach to fitting and selecting models, we intended to balance the relative strengths and weaknesses of several criteria for evaluating models. By emphasizing predictive performance for model selection measured with RPI from spatial cross-validation, we aimed to emphasize generalizable relationships and avoid over-fitting models to specific locations (Guisan and Thuiller 2005). Indeed, the best-fitting model (with lowest AIC) for a species was often not the most predictive (or selected) model, and selected models instead emphasized covariate relationships that
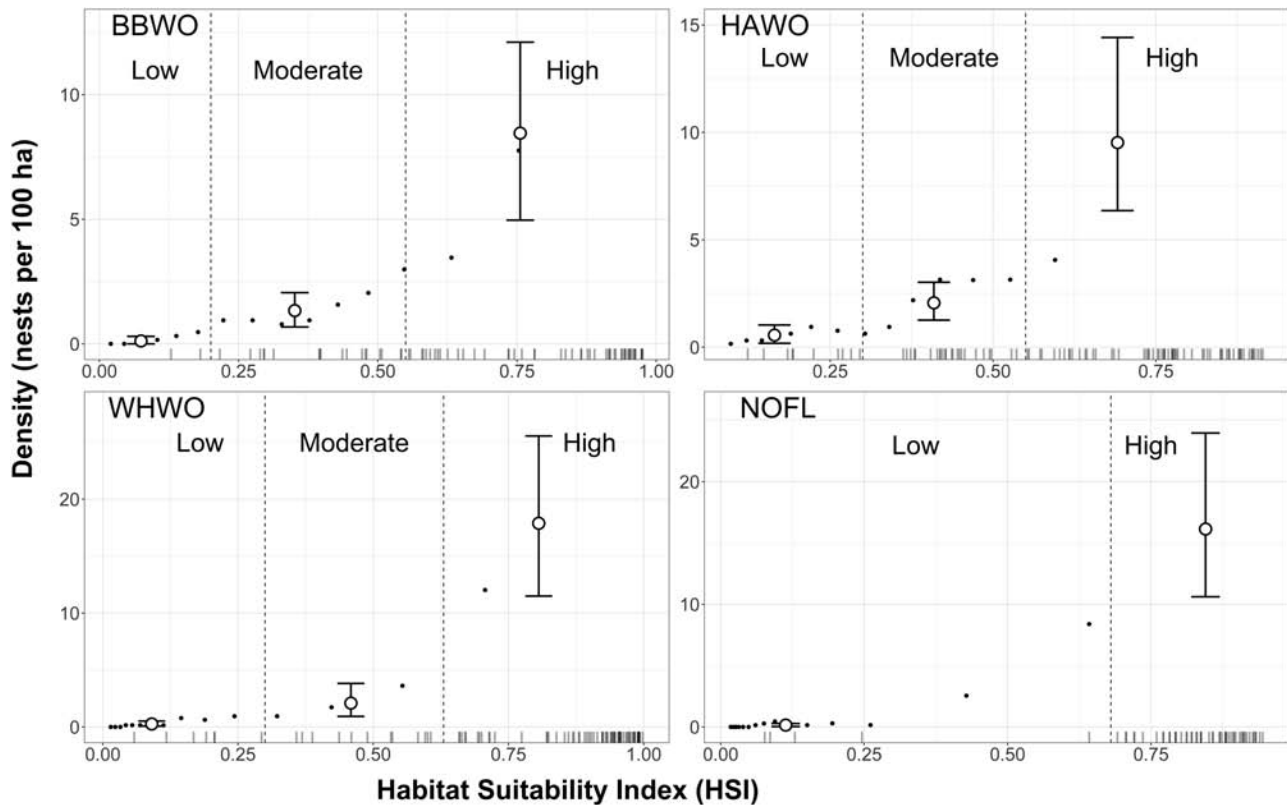
FIGURE 3. Nest densities plotted against HSI for equal-*n* moving-window bins (small black dots) and HSI-based suitability categories of low, moderate, and high (large open circles) for combination models. Data rugs represent nest sites.

were consistent across locations. Despite the strong theoretical rationale for selecting models based on predictive performance (Wiens et al. 2008, Heikkinen et al. 2012, Wenger and Olden 2012, Hooten and Hobbs 2015), criteria that explicitly measure predictive performance typically lack clear interpretation for model selection. Authors who use predictive performance to select models therefore inevitably develop and employ their own criteria suited to their particular needs (e.g., Wiens et al. 2008, Hooten and Hobbs 2015). We therefore supplemented RPI with a more explicitly established criterion for model selection to identify and screen the worst-fitting models (ΔAIC > 6, i.e. evidence ratio < 0.05 relative to the highest rank [lowest AIC] model; Burnham and Anderson 2002). Additionally, we further avoided overfitting models to our data by excluding covariate relationships that were not clearly supported (i.e. Parsimony criterion, Table 4; see also Wiens et al. 2008). Finally, because we wanted models that reliably classified suitable nest-site habitat correctly, we excluded models that did not consistently assign relatively high HSI values to nest sites across our study locations (i.e. Sensitivity criterion, Table 4). Our results may be sensitive to the particular set of criteria we employed for selecting models. Given the above rationale, however, we are confident that selected models will be reasonably suited to the purpose

of identifying likely woodpecker nesting habitat within newly burned forest. We encourage further work toward integrating methods for selecting models and evaluating predictive performance.

Although our study locations represent common conditions for woodpeckers selecting nests in larger fires of the region, in an effort to maximize predictive performance, we did not add salvage logging intensity to our models over concern that doing so could cause over-fitting. Salvage logging of nearly all snags and live trees with a chance of dying occurred within a year of the fire on most private lands, which is typical of private inholdings across Sierra Nevada, while more selective harvest of snags and no live trees occurred on public lands. The area logged was highest at Moonlight (inside and within 1 km of surveyed transects), followed by Chips (outside of surveyed transects, within 1 km), and negligible in extent at Cub. The strong predictive performance across study locations suggests model predictions may be robust to moderate levels of salvage logging, but we expect poor model transferability to more extensively logged areas. Salvage logging changes availability and distribution of resources, potentially altering species' habitat relationships (Peterson et al. 2009, Saab et al. 2009). Additionally, salvage logging may render remotely sensed pre-fire forest structure variables less informative
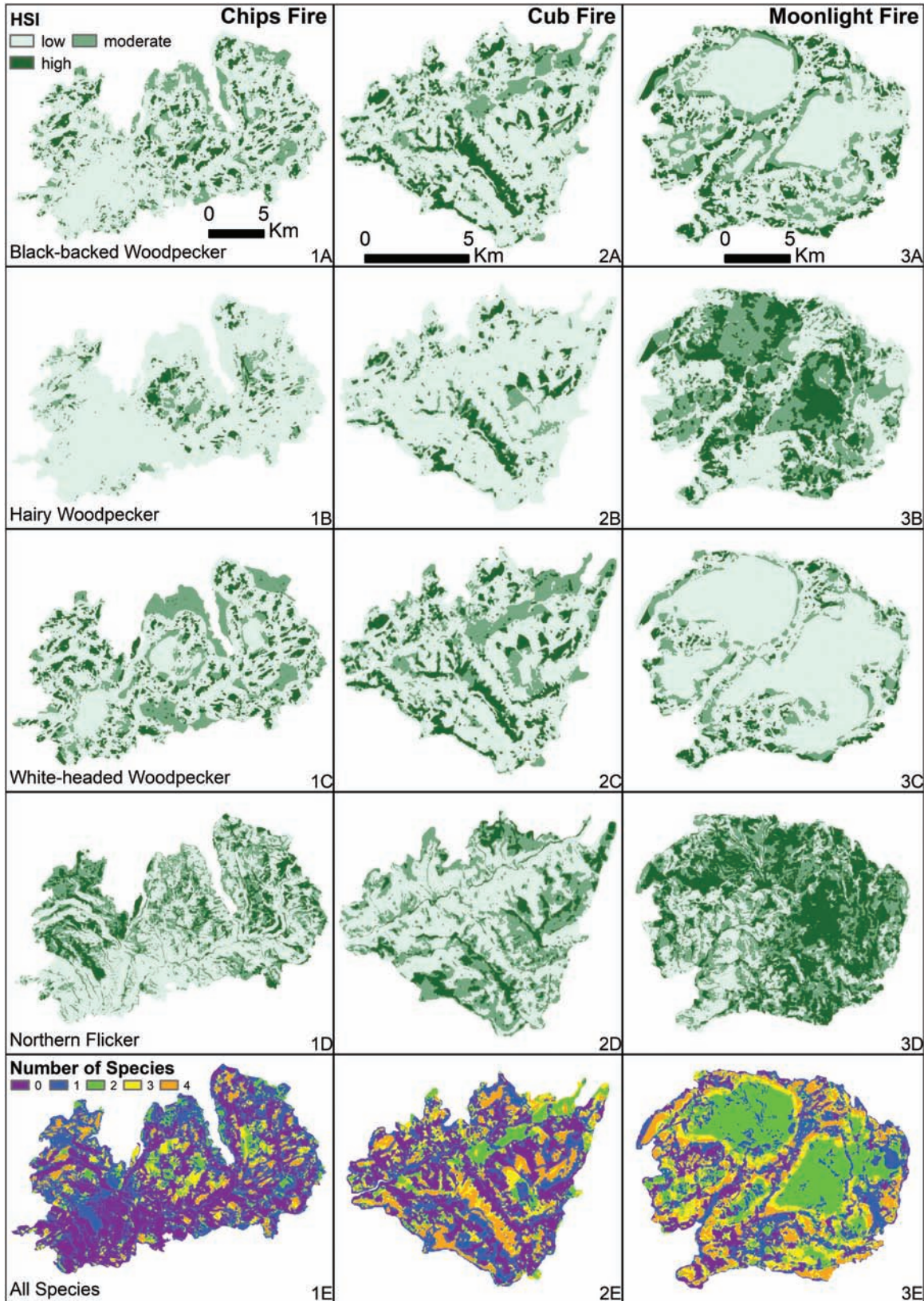
FIGURE 4. Predictions of woodpecker nesting habitat suitability derived from remote-sensing models for 3 (columns 1–3) wildfire study locations. Rows A–D represent individual species, while row E maps the number of species with moderate- or high-suitability habitat.

by distorting the relationship between covariates and post-fire conditions (e.g., snag diameters and densities; Russell et al. 2007).

Implications for Forest Management

We provide predictive nest-site habitat models to identify areas of conservation for nesting woodpeckers in post-fire forests of the Northern Sierra Nevada. Models restricted to remotely sensed covariates are useful for mapping habitat across entire wildfire locations. Mapped model predictions can help managers identify areas of high-suitability nest-site habitat where conservation would be most beneficial, as well as areas of lower suitability where management actions such as salvage logging would minimally impact nesting habitat (Figure 4). Moreover, overlaying maps for multiple species could help identify areas of conservation value for multiple disturbance-associated woodpeckers along with other associated habitats and species (Figure 4). To these ends, Latif et al. (2018) developed the FIRE-BIRD ArcGIS toolbox to help forest managers across the western United States translate woodpecker habitat suitability models into GIS-compatible map layers, including the remote-sensing models in this study, to recently burned areas. Unlike others (Russell et al. 2007, Latif et al. 2016), we found similar predictive performance with models restricted to remotely sensed data compared to those that included field measurements (but see Northern Flicker). Thus, we are particularly confident in the value of models here for predicting nesting distributions with only remotely sensed data. Nevertheless, models with field-collected data provide information especially relevant for finer-scale prediction and design of management prescriptions (i.e. snag sizes, densities, and condition; Peterson et al. 2009). For example, salvage prescriptions could be informed by the relationships with DBH and snag condition taken from our combination models to guide the retention of highly suitable woodpecker nest trees. Higher-resolution remotely sensed data (e.g., LiDAR; Lefsky et al. 2002) could also enable spatial predictions using the combination models.

Our findings have implications for forest management in the Northern Sierra Nevada both before and after wildfire. Patches of dense snags after wildfire represent important conservation targets for Black-backed Woodpecker (Saab et al. 2009, Seavy et al. 2012, Siegel et al. 2018). For other species, retaining relatively large broken-topped snags may help limit negative impacts of selective logging. Additionally, because broken-topped snags immediately after wildfire were likely killed pre-fire, snags in green forest increase in value for nesting woodpeckers with future wildfires (e.g., Saab and Dudley 1998).

Our models also inform conservation of habitat within 1 km of nests. Mosaics of various burn severities were important for Black-backed and White-headed woodpeckers.

Dense areas of smaller trees and snags (whether burned or unburned) were important habitat surrounding Hairy Woodpecker nest sites.

We likely avoided AIC-associated bias favoring complex models (Link and Barker 2006) by selecting models based on predictive performance. Conversely, selected models may not fully describe all relevant components of suitable nesting habitat. Consequently, selected models alone are not adequate for informing design of management prescriptions. For example, although selected models did not include snag density, positive relationships with this feature were supported in other models for Black-backed and Hairy woodpecker. Additionally, snag densities were generally higher for all species at nest compared to non-nest sites, suggesting intensive logging is generally detrimental to nesting woodpeckers (see Table 5). Along with models selected for prediction, descriptive statistics and covariates appearing in other strongly performing models are useful when designing silvicultural prescriptions. Additionally, although correlative studies are informative, experimental data are ultimately needed for complete knowledge of habitat requirements relevant to management (Buckland et al. 2009, Latif et al. 2012).

We related HSIs and derived suitability categories (low, moderate, and high) with observed nest densities to aid interpretation when informing management. Density estimates with bootstrapped confidence limits indicated variation in densities among the suitability classes. We expect density estimates to correctly represent the magnitude of change along HSI gradients, although we did not correct for detectability. In so far as alternative management scenarios are expected to affect HSI, managers can use these relationships to gauge implications for nesting density.

content of the submitted or published manuscript. None of our funders require approval of the final manuscript to be published. Use of trade names does not imply endorsement by the U.S. Government.

Conflict of interest statement: The authors declare that they have no conflicts of interest.

Ethics statement: The authors adhered to the Point Blue policy on scientific ethics. The views in this article are those of the authors and do not necessarily reflect those of their employers.

Author contributions: R.B. and B.C. conceived the idea, design, experiment (supervised research, formulated question or hypothesis). R.B. and B.C. performed the experiments (collected data, conducted the research). B.C., Q.L., R.B., and V.S. wrote the paper. Q.L., B.C., R.B., and V.S. developed or designed the methods. Q.L. and B.C. analyzed the data.

Data depository: Analyses reported in this article can be reproduced using the data in Zenodo (https://doi.org/10.5281/zenodo.3354378).

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APPENDIX A

Calculation of RPI for quantifying predictive performance
  We calculated resource selection function plot index (RPI) following Wiens et al. (2008). For each species, we calculated RPI for each wildfire location withheld from model fitting as follows:

1. Apply the HSI model to the withheld data.
2. Normalize HSI values by subtracting the minimum value and dividing by the range: $HSI_{norm} = (HSI - HSI_{min}) / (HSI_{max} - HSI_{min})$.
3. Sort all nest and non-nest observations by HSI_{norm}.
4. Bin observations into 10 equal-n moving-window bins, that is bins equal in the number of observations and that overlap with neighboring bins along a gradient of HSI_{norm} values. Because the target number of bins is 10 for all datasets, the number of observations in each bin and the amount of overlap with neighboring bins depends on sample size of the dataset. We list bin sizes and levels of overlap for each dataset in Appendix Table 9.
5. Calculate observed and predicted values for each bin, where observed bin values are the proportion of nests (number of nests divided by the sum of nest and non-nest locations in each bin) and predicted bin values are the mean for HSI_{norm}.
6. Calculate RPI – the Spearman's rank correlation coefficient relating observed with predicted bin values ($n = 10$).

APPENDIX TABLE 9. Moving-window bin structure for calculating RPI values. For each nesting species (Black-backed Woodpecker [BBWO], Hairy Woodpecker [HAWO], White-headed Woodpecker [WHWO], Northern Flicker [NOFL]), the table reports the total number of sites (n = nest + non-nest) at each wildfire location, the number of sites in each moving-window bin, and the number of sites shared between neighboring bins (overlap).

			Bin structure	
Fire	Nesting species	n	n [a]	overlap
Moonlight	BBWO	361	96	64
	HAWO	320	84	56
	WHWO	355	90	60
	NOFL	344	90	60
Cub	BBWO	119	30	20
	HAWO	106	27	18
	WHWO	132	33	22
	NOFL	115	30	20
Chips	BBWO	69	18	12
	HAWO	64	20	15
	WHWO	83	28	21
	NOFL	79	28	14

[a] Most datasets were not evenly divisible by the bin size listed, so the 10th bin typically contained fewer observations than sizes listed here for bins 1–9.

APPENDIX B

Summary and descriptive statistics for nest and non-nest sites.

APPENDIX TABLE 10. Number of nests across wildfire locations (Moonlight, Cub, Chips) and years post-fire used to model nesting habitat suitability. Nests are for Black-backed Woodpecker (BBWO), Hairy Woodpecker (HAWO), White-headed Woodpecker (WHWO), and Northern Flicker (NOFL). NA indicates data not collected.

		Number of nests				
Fire	Nesting species	1 yr post-fire	2 yr post-fire	3 yr post-fire	4 yr post-fire	5 yr post-fire
Moonlight	BBWO	NA	2	8	7	7
	HAWO	NA	5	19	6	16
	NOFL	NA	4	11	4	10
	WHWO	NA	5	12	5	8
Cub	BBWO	0	9	5	5	NA
	HAWO	4	8	8	7	NA
	NOFL	3	5	5	4	NA
	WHWO	2	7	3	8	NA
Chips	BBWO	8	7	8	5	NA
	HAWO	5	7	5	7	NA
	NOFL	1	3	4	3	NA
	WHWO	16	9	8	5	NA

APPENDIX TABLE 11. Descriptive statistics (mean [SD, min–max] or proportion for categories) for habitat variables used for HSI models for nesting woodpeckers following wildfire. Non–nest site values represented include sites <130 m from nests and centered on live trees (n = 849) that were later excluded or filtered for analysis. Nests are for Black-backed Woodpecker (BBWO), Hairy Woodpecker (HAWO), White-headed Woodpecker (WHWO), and Northern Flicker (NOFL). Non-nest values are separated by wildfire location (Cub, Chips, and Moonlight) for comparison. For variable descriptions, see Tables 2 and 3.

| Variable	Nest sites				Non-nest sites		
	BBWO (n = 71)	HAWO (n = 97)	WHWO (n = 88)	NOFL (n = 57)	Cub (n = 389)	Chips (n = 194)	Moonlight (n = 1,251)
SLOPE	17.8 (9.6, 4–50)	18.6 (10.8, 1.4–54.7)	20.2 (12.9, 4–70.9)	16.8 (8.4, 2.6–36.1)	25.1 (12.7, 4.7–66.7)	15.7 (10, 3.2–45.8)	21.3 (11.4, 1.7–69.2)
SASP	0.2 (0.7, –1 to 1)	0.2 (0.7, –1 to 1)	0.3 (0.7, –1 to 1)	0.1 (0.7, –1 to 1)	–0.1 (0.7, –1 to 1)	0.3 (0.6, –1 to 1)	0 (0.7, –1 to 1)
CASP	0 (0.7, –1 to 1)	0.1 (0.7, –1 to 1)	0.1 (0.7, –1 to 1)	0 (0.8, –1 to 1)	0.5 (0.6, –1 to 1)	0.1 (0.7, –1 to 1)	0 (0.7, –1 to 1)
LocBurn	72.8 (37, 0–100)	78.4 (33.2, 0–100)	60.1 (41.2, 0–100)	67.5 (38.7, 0–100)	14.1 (25.7, 0–100)	26.3 (38.9, 0–100)	60.9 (41.6, 0–100)
LandBurn	33.2 (30.3, 0.8–99.9)	41.6 (35.8, 0.3–99.9)	26 (25.9, 0.4–99.8)	40.3 (34.6, 0.6–99.8)	12.7 (8.4, 0.4–36.9)	9.3 (8.8, 0.3–28.8)	60.2 (25.6, 0.6–99.9)
LocCC	94.8 (15.6, 22.2–100)	89 (28.4, 0–100)	78.3 (37.1, 0–100)	77.6 (39, 0–100)	87.6 (28.9, 0–100)	65.9 (41.7, 0–100)	84.8 (31.2, 0–100)
LandCC	79.3 (15.8, 47.6–99.1)	84.4 (13.5, 47.8–99.1)	79.4 (14, 44.7–97.5)	81 (16.7, 44.4–100)	88.3 (8.7, 57.9–100)	73.6 (15.4, 51.9–97.9)	81.2 (13.5, 39.9–99.1)
LocSizeSm	61.5 (47, 0–100)	46.2 (45, 0–100)	53.2 (46.9, 0–100)	38.8 (43.9, 0–100)	46.8 (44.3, 0–100)	63.1 (42.8, 0–100)	23.8 (37.9, 0–100)
LandSizeSm	54 (27.4, 3.6–98.2)	41.8 (27.8, 2.9–96.3)	54.2 (27.1, 4.3–97.9)	36.9 (26, 3.5–96.1)	44.9 (16.5, 17.9–84.5)	67.9 (18.7, 33.3–97.7)	26.2 (17, 2.6–75.4)
LocSizeLrg	32.6 (44.2, 0–100)	45.5 (45.4, 0–100)	29.2 (42.3, 0–100)	38 (43.7, 0–100)	42.7 (42.6, 0–100)	22.7 (39.1, 0–100)	59.3 (44.6, 0–100)
LandSizeLrg	31.4 (27.2, 0–92.9)	45.9 (29.7, 0–94.3)	32.8 (24.9, 0–93.6)	47.2 (29.1, 0–93.7)	44 (16.7, 7.7–79.8)	19.6 (19.8, 0–54.1)	54 (21.2, 13.8–94.1)
LandFir	27.3 (31.7, 0–87.3)	14.9 (23.5, 0–87.4)	19.6 (25.7, 0–81.7)	11.9 (24.6, 0–81.6)	12.8 (13.4, 0–43.9)	38.5 (34, 0–87.7)	8.9 (14.6, 0–57.4)
DBH	36.1 (10.9, 18–69)	41.4 (17.1, 20–146)	54.8 (27.9, 16–164)	54.2 (26.9, 26–139)	37 (23.4, 1–127)	38.9 (20.2, 13–110)	37.2 (23.7, 6–142)
TreeSpPine	0.31	0.3	0.33	0.16	0.14	0.14	0.26
TreeSpFir	0.68	0.64	0.56	0.79	0.76	0.81	0.62
BRKN	0.21	0.55	0.78	0.93	0.09	0.18	0.15
SnagDens23to50	7.4 (5.4, 0–22)	5.2 (5.1, 0–24)	4.5 (4.5, 0–21)	3.9 (3.7, 0–20)	3.4 (5.2, 0–38)	3.7 (4.4, 0–20)	2.9 (3.2, 0–22)
SnagDensGT50	1.7 (2.3, 0–10)	1.4 (1.9, 0–8)	1.8 (1.7, 0–7)	1 (1.2, 0–5)	0.7 (1.3, 0–8)	1.3 (2.1, 0–11)	0.9 (1.4, 0–7)
SnagDensGT23	9.1 (6.6, 0–23)	6.6 (6, 0–27)	6.2 (5.3, 0–22)	4.9 (4.1, 0–20)	4.1 (5.6, 0–38)	5.1 (6.1, 0–30)	3.7 (3.8, 0–22)
PineDens	1.5 (2.8, 0–15)	1.1 (1.8, 0–9)	1.2 (2.1, 0–11)	0.7 (1.4, 0–8)	0.3 (0.8, 0–6)	0.6 (1.4, 0–8)	0.8 (1.5, 0–10)
FirDens	7.4 (6.4, 0–22)	5 (6.1, 0–27)	4.7 (4.6, 0–21)	3.8 (4.1, 0–20)	3.6 (5.4, 0–37)	4.3 (5.4, 0–26)	2.6 (3.3, 0–18)

APPENDIX C

HSI relationships with covariates for models restricted to remotely sensed data. Each plot shows the relationship with a given covariate from the minimum to maximum observed values while holding all other covariates in the model at their mean values for nest and non-nest sites. Gray shading indicates 95% confidence intervals. Horizontal dotted lines indicate HSI thresholds for classifying low-, moderate-, and high-suitability habitat suggested from density plots (Figure 2). Complete covariate names, descriptions, and units are in Table 2.
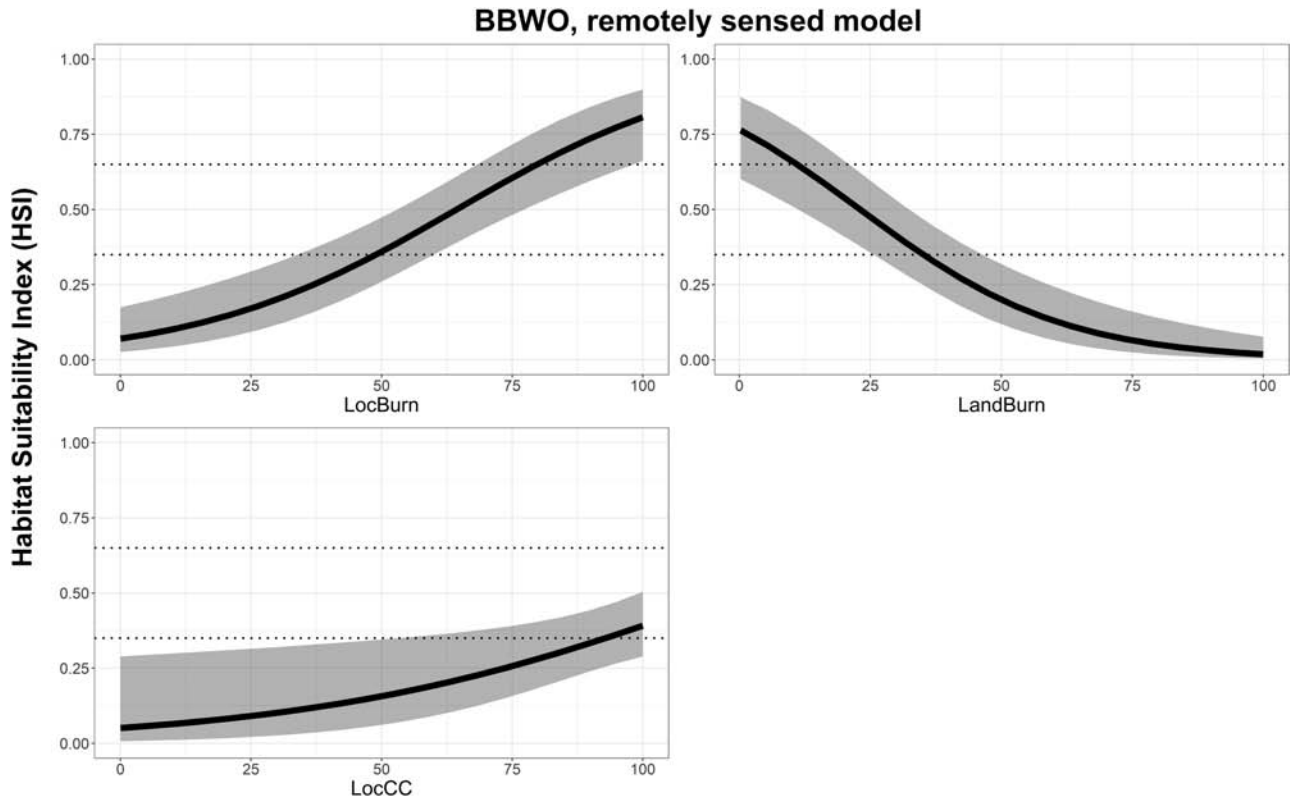
Appendix Figure 5. Black-backed Woodpecker remotely sensed model.
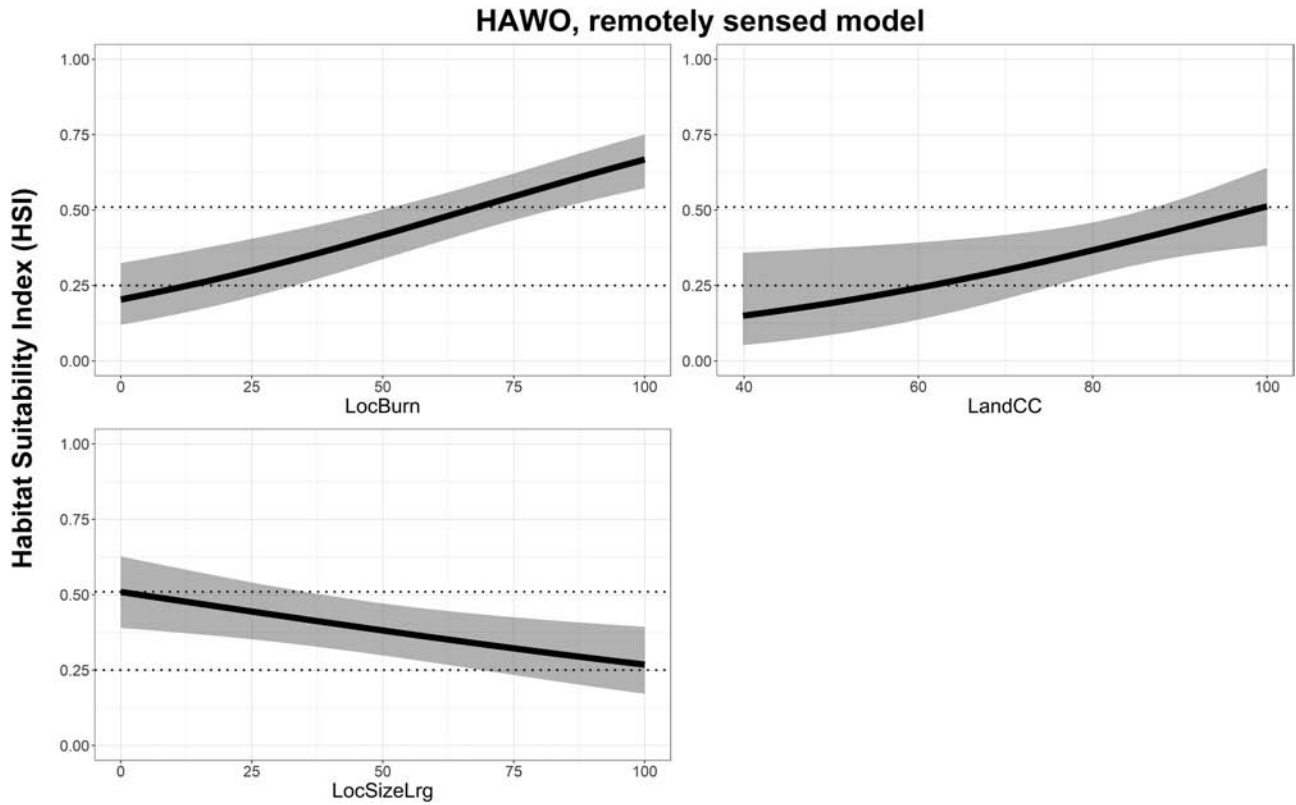
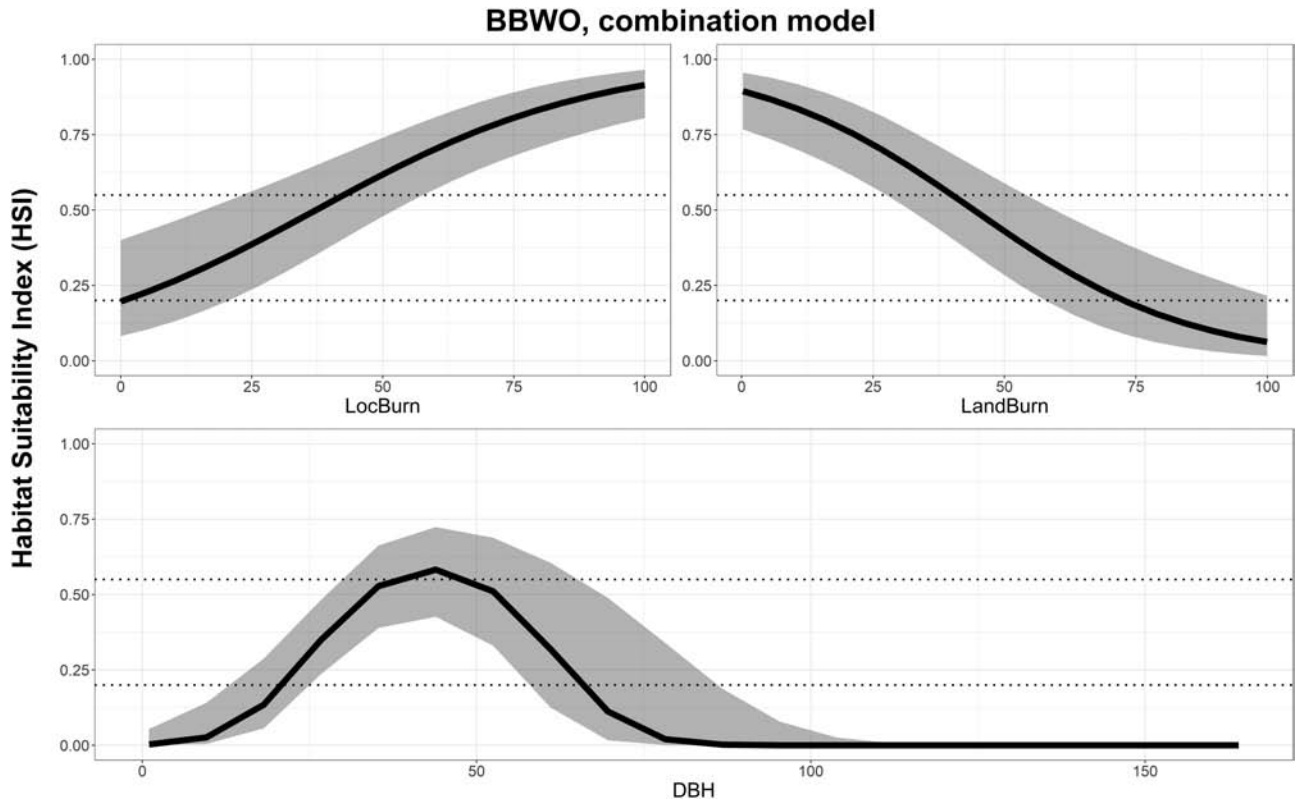**Appendix Figure 6.** Hairy Woodpecker remotely sensed model.
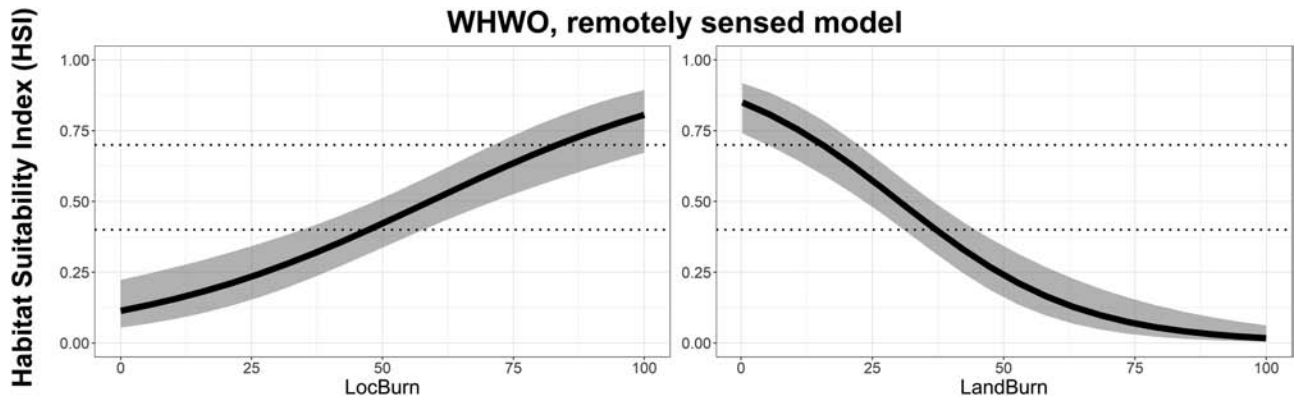
Appendix Figure 7. White-headed Woodpecker remotely sensed model.
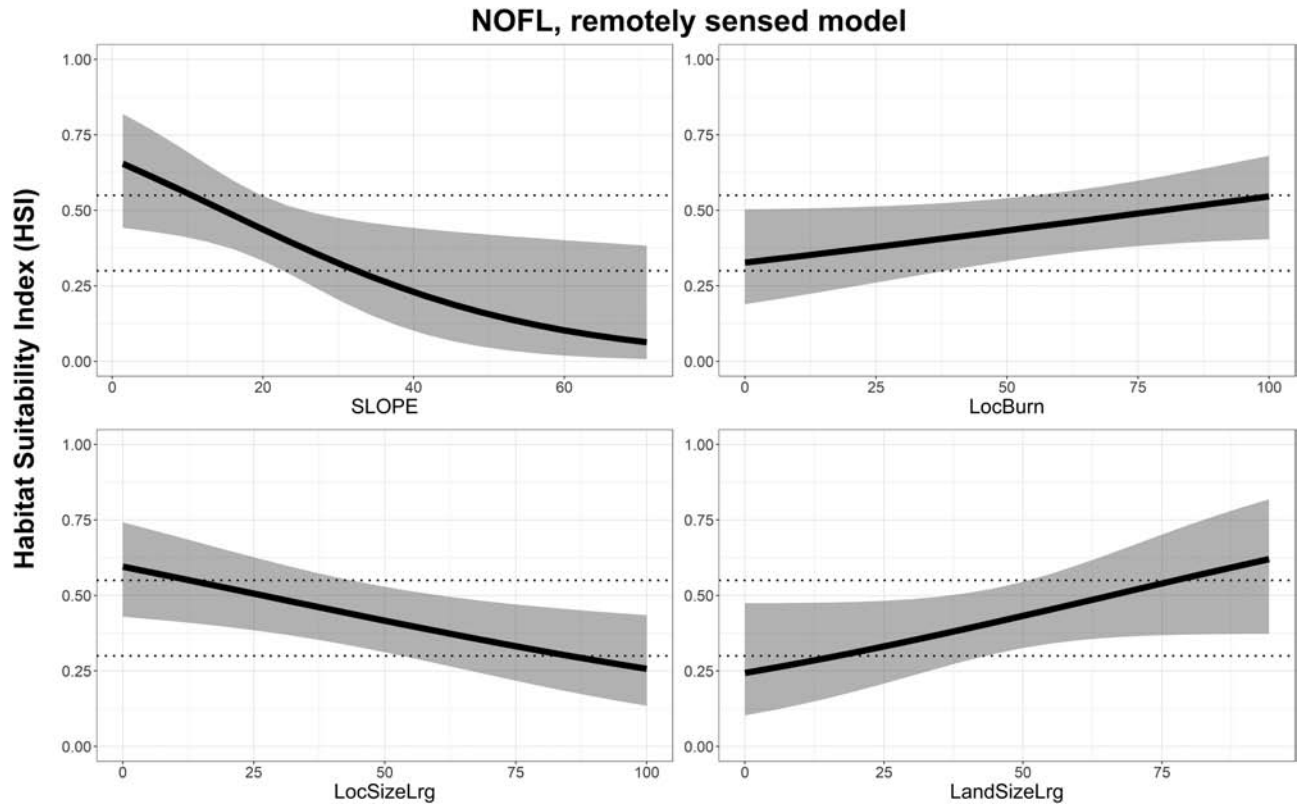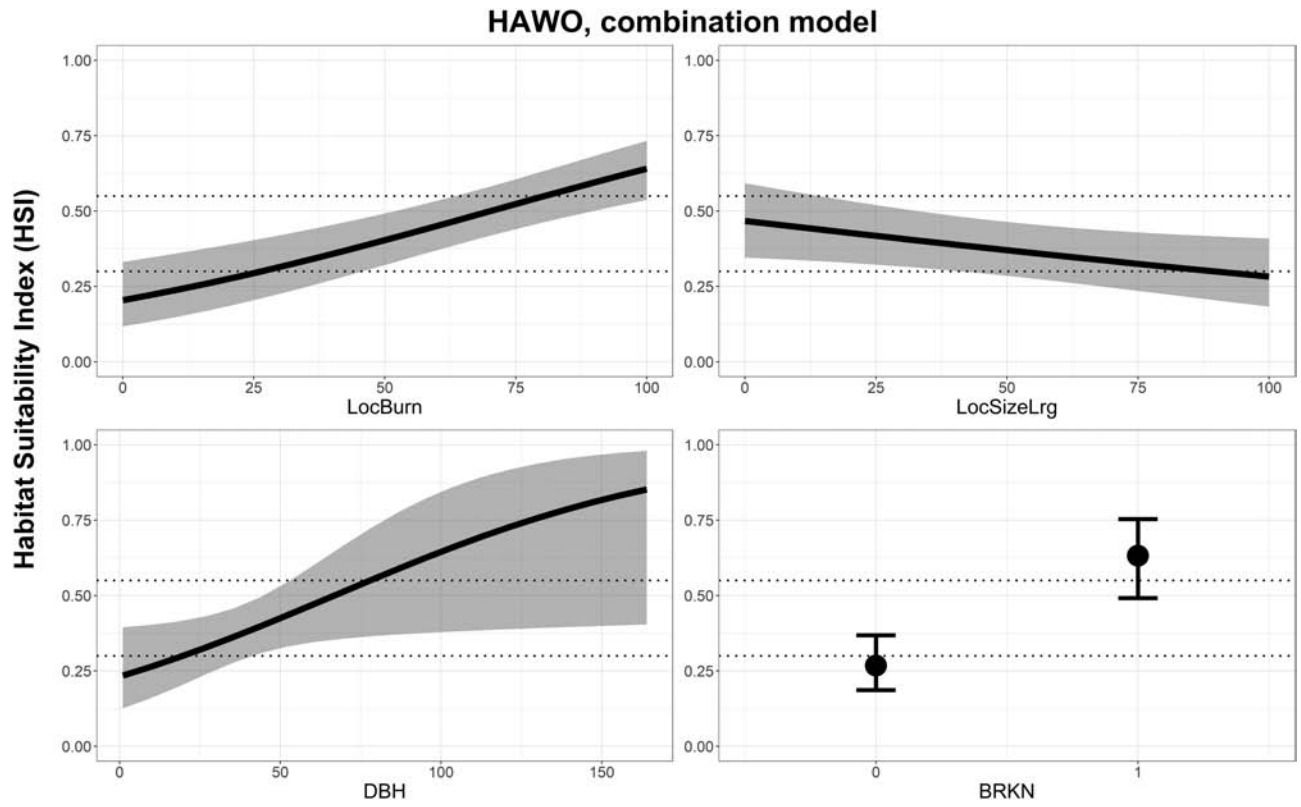
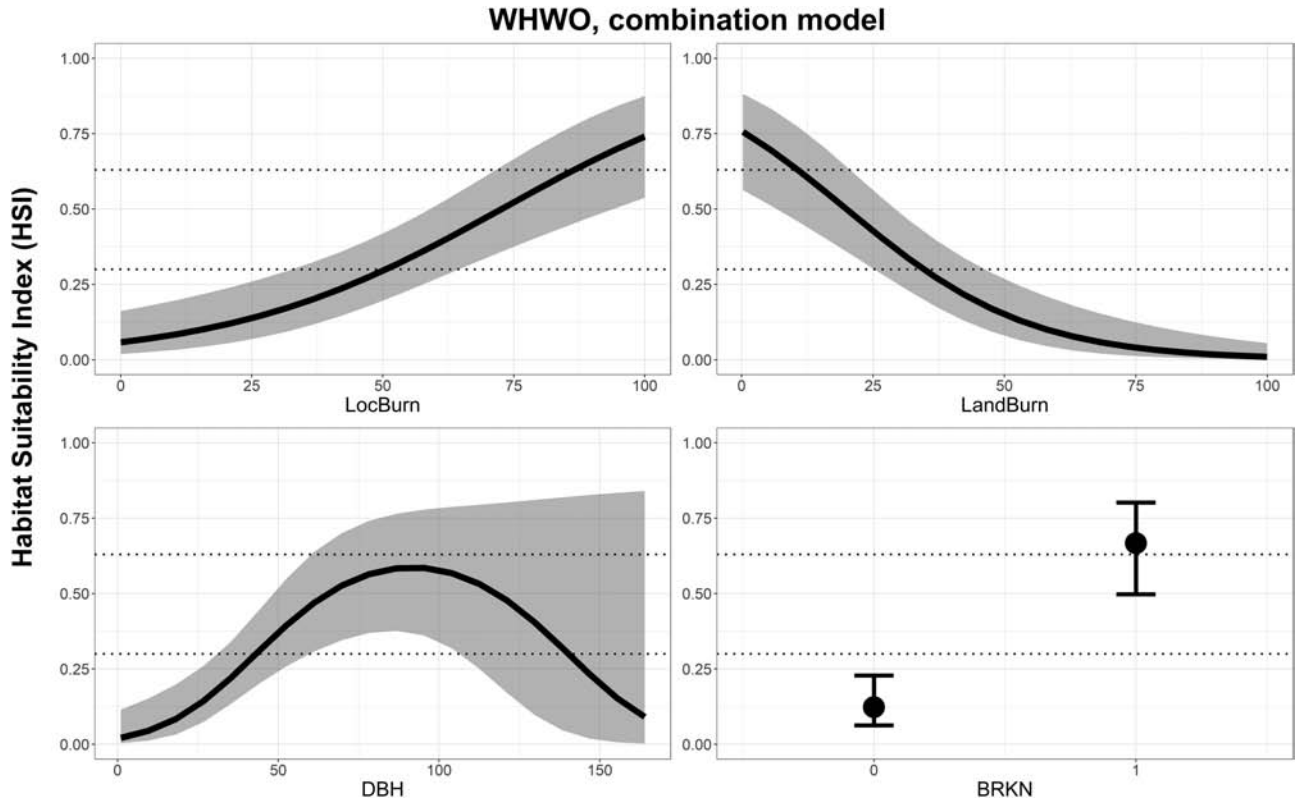**Appendix Figure 8.** Northern Flicker remotely sensed model.

APPENDIX D

HSI relationships with covariates for models that included remotely sensed and field-collected data (combination models). Each plot shows the relationship with a given covariate from the minimum to maximum observed values while holding all other covariates in the model at their mean values for nest and non-nest sites. Gray shading indicates 95% confidence intervals. Horizontal dotted lines indicate HSI thresholds for classifying low-, moderate-, and high-suitability habitat suggested from density plots (Figure 3). Complete covariate names, descriptions, and units are in Table 2.
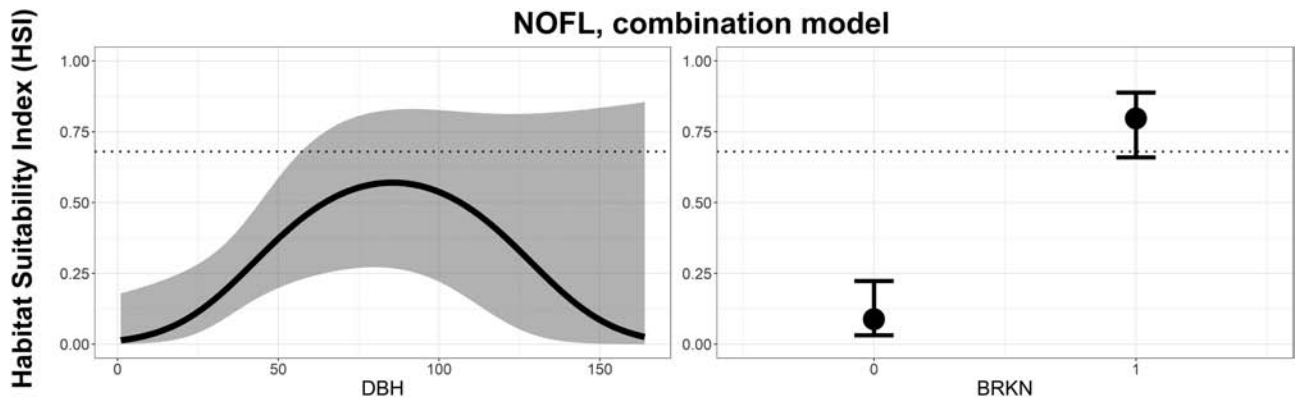

Appendix Figure 9. Black-backed Woodpecker combination model.

Appendix Figure 10. Hairy Woodpecker combination model.

Appendix Figure 11. White-headed Woodpecker combination model.

Appendix Figure 12. Northern Flicker combination model.